The Effects Of Limpet Grazing On Algal Colonisation Around The Coast Of Holy Island (Anglesey)

Thesis

UNRESTRICTED

"THE EFFECTS OF LIMPET GRAZING ON ALGAL COLONISATION AROUND THE COAST OF HOLY ISLAND (ANGLESEY)"

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ABSTRACT

Limpets are common on exposed shores where they are generalist feeders of algal sporelings and mature plants. They are known to be responsible for the paucity of algal cover on exposed shores. The cyclic relationship which may exist between algae and limpets is probably partly controlled by the degree of exposure of the shore.

Five experimental areas differing in aspect and degree of slope, were chosen on the exposed rocky shore of the West coast of Holy Island (Anglesey). The experimental areas were cleared of limpets to allow algal colonisation to take place. Adjacent control areas were however not cleared of limpets and grazing continued in these areas. Any changes in algal composition in both experimental and control areas were monitored by using quantitative methods.

The pattern of recolonisation and algal succession on sheltered shores as described by previous workers, such as Jones (1946) was confirmed. Algal zonation occurred on almost all experimental areas and there was no strong evidence for zone mixing as described by Lodge (1948). Some alteration in the distribution of certain members of the Rhodophyceae indicated increased moisture levels on the rock surface as a result of recolonisation.

There was also some evidence of greater species diversity

on the experimental areas compared with the control areas. Algal composition however, remained virtually unchanged in the control areas even after three years of study.

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1. INTRODUCTION

The interaction between plants and animals in particular the effects of grazing on plant productivity and distribution have been a major preoccupation of ecologists for over sixty years. Grazing occurs in both marine and terrestial environments and the phylum Mollusca contains examples of both marine and terrestial grazers. This study is concerned with the marine grazing animal Patella vulgata L. (Common Limpet) and its impact on the algal flora of rocky shores of different degrees of exposure.

1.1 Limpet grazing and algal colonisation

Limpets are Gastropod molluscs belonging to the order: Prosobranchiata. Patella vulgata is found in the eulittoral zone on rocky shores, clinging to the rock surface at a specific "home" site when exposed at low tide and moving slowly across the surface of the rock when under water. Limpets possess a muscular foot for locomotion and clinging to the rock surface. During locomotion they feed on plant material on the rock surface. Fischer - Piette (1948), Jones (1946) and Orton (1914) observed that the radula is moved backwards and forwards over the rock surface rasping off particles of food, detritus and rock.

Hatton (1938) observed that limpets are more numerous on exposed, rocky shores than on sheltered seaweed - covered ones.

Several theories have been put forward to explain low limpet numbers on sheltered shores, e.g., the difficulty for spat of settling between algal fronds, silting and clogging up of gills due to slower currents and reduced wave action, also the sweeping action of large fucoids. (Jones 1946). The high limpet density on exposed rocky shores was found to be associated with a rather sparse algal cover (Jones 1946).

At first, exposure and extreme wave action were suspected of causing this, but there is now strong evidence that limpet grazing is the main cause of low algal cover on these shores (Jones 1946).

Moore (1938) observed that the sides of a swimming pool covered by algae (Enteromorpha spp., Porphyra spp., etc.) were rapidly cleared once limpets began to feed on them. These limpets were found to be feeding not only on mature plants but also on young algal sporelings. Prior to this work Moore had, in 1936, already studied the grazing area required by limpets. He estimated that a limpet aged one year required a feeding area of a least 75 cm^2 per cm^3 body volume in order to stay alive. It is obvious from these observations that the limpet population of an exposed rocky shore (where the population density can exceed numbers of over a hundred limpets per square metre), would graze a tremendous quantity of material per year.

Other studies on the feeding behaviour of limpets were carried out separately in 1948 by Fischer - Piette and Jones, both of whom concluded that P. vulgata will feed actively on the algae growing on the rock surface. Fischer - Piette (1948) stated that the limpets feed on the brown fucoid seaweeds and thereby cause their destruction. Jones (1946) on the other hand had observed that the limpets grow well even on apparently bare rock surfaces where there is little recognisable food. He concluded that the animals feed on microscopic algal sporelings as well as on mature plants. He also noted that there was a definite link between the number of limpets on the rock surface and the amount of algae growing on the same surface: the greater the number of limpets the sparser the algal cover. He concluded that there must be some formof ecological balance between the limpet and algal populations.

Evidence that limpets actually feed on algae was provided by Jones (1946) when he examined the stomach contents of some of the limpets. In areas of the shore where the limpets lived near fucoid algae, the gut contents were found to be full of brown fucoid particles. Limpets living near green Enteromorpha spp. were found to have their gut full of green particles. These results provided concrete evidence that limpets are generalist browsing animals feeding on whatever is close at hand.

Southward (1964) stated that limpets feed at high tide or when conditions are moist, at low tide. They graze mainly on unicellular and filamentous algae, an important source of food on an exposed shore. Laboratory experiments carried out by Southward did not indicate any food preferences shown by limpets. They grazed red, brown and green algae but rejected the brown algae Ralfsia spp. Limpets were also shown to graze mature fucoid plants, grazing thallus, midrib and holdfast with the result that the damaged plants were carried away by heavy wave action.

Southward confirmed Jones' (1946) statement that limpets were abundant and algae scarce on exposed shores. He believed that wave action operated indirectly on algal growth by encouraging large numbers of limpets to settle and graze the algae present on the rock surface. Exposure to wave action was believed to reduce the clogging up of limpet gills by silt and encourage the growth of small food algae. Southward thought it possible that the reason why bare rocky surfaces supported such a high density of limpets was that the limpets had to spend so much time and energy clinging to the substratum because of wave action, that they did not spend so much time grazing and therefore grew slowly and remained small in size.

Although the availability of food is probably an important factor controlling the population density of limpets, the amount of light and heat received by the rock surface is

also important. Lewis (1954) observed that limpets will migrate downwards towards low water during the summer and then migrate back towards high water mark during the winter. This behaviour decreases the risk of desiccation during the summer months.

To assess the impact of limpet grazing on algae, experiments have been carried out in which limpets were cleared from areas of bare, rocky shore and any subsequent algal growth monitored. Some authors observed a definite sequence in the species re-colonising grazed areas.

In April 1936 Pyefinch cleared the limpets from a series of rock surfaces along the coast of Bardsey Island, Gwynedd. Six surfaces, each approximately one square yard in area were cleared of all fauna and flora (including presumably the removal of limpets). The cleared areas were selected from different algal zones such as the Fucus spiralis zone (near High Water Spring) down to the Corallina/Lithophyllum zone (near Low Water Spring). Pyefinch states that in one of the cleared areas the re-colonising algae formed a succession. The first colonists to grow on the bare rock surface were several green algae e.g., Ulva lactuca. Later the green algae were succeeded by brown Fucus spiralis which eventually covered the rock surface at the expense of the green algae. This succession of green to brown algae was also observed to a lesser extent on the other experimental areas. However, Pyefinch states that this succession of green to brown algae does not seem to be

an essential stage in the colonisation of a bare rock surface.

Jones (1946) also presented some observations on the growth of algae following the clearance of limpets from a rock surface. An experimental area five metres square was selected on the coast of the Isle of Man. There were no algae present but there was a dense cover of barnacles and a fairly dense population of limpets. All limpets were removed from the experimental area in August, 2184 in all, varying in size from 16 mm to 30 mm in shell length. By April of the same year algal sporelings were establishing themselves on the cleared area and by June a thick felt of mainly green algae had developed. Jones observed that a few limpets had migrated back into the experimental area and were grazing the green algae. These green algae gradually disappeared and were largely replaced by brown Fucus vesiculosus. Apparently the F. vesiculosus was protected to some extent in its early stages by the green algae.

A similar study was carried out by Eslick in 1937, when a smaller area of rock was cleared of limpets and algae allowed to re-colonise the rock surface. A thick covering of F. vesiculosus developed on the cleared area. There was little evidence for limpet grazing in this particular area probably due to the irregular outline of the rock. Eslick concluded that the F. vesiculosus will develop normally despite migration back of the limpets into the

experimental area provided it is protected from grazing during the early stages of its growth.

These observations by Pyefinch, Jones and Eslick provide strong evidence that:-

(a) algae will re-colonise rock surfaces cleared of limpets.

(b) a type of algal succession occurs following limpet clearance, green algae being succeeded by brown, particularly F. vesiculosus.

Lodge (1948) demonstrated that the above observations were also true for larger areas of rock surface. During October 1948 she cleared a strip of shore ten metres wide from just below Mean High Water Spring Tide to just above Mean Low Water Spring Tide. The experimental area was situated on the limestone terraces at Port. St. Mary, Isle of Man. A few weeks after the limpets were cleared from the strip, small algal sporelings mainly of green algae had established themselves. These grew strongly until, by April, they formed a bright green strip on the rock surface. The brown F. vesiculosus then began to establish itself along most of the cleared area. This alga was joined at the same time by another brown colonist F. serratus. Eventually the green algae were replaced almost entirely by the larger brown algae. It was also noted that some of the more delicate red algae e.g., Dumontia incrassata extended their range higher up the shore in the experimental area than in the surrounding grazed areas. This was probably due to

protection from desiccation by the larger fucoid plants.

The limpets were allowed to return to the experimental strip and although a thick growth of alga covered almost 100% of the experimental area, it was found that the limpets were gradually removing the green alga and the sporelings of the brown alga by their grazing activity. Lodge believed that the strip would eventually return to its original state, although it would take some time for the limpets to graze through the holdfasts of the mature Fucus plants. One interesting side effect of the re-colonising of a bare rock surface seems to be the high incidence of hybrids between the Fucus spp.

In Lodge's experiment (1948) she reported that the limpets which eventually moved into the dense fucoid growth of the experimental areas, were young animals migrating in from nearby areas, feeding and growing rapidly on the abundant food supply. There were six times as many limpets on the re-colonised experimental areas than there were previously. It was observed that few adult limpets migrated in. Within seven years the experimental areas had returned to their former condition (Lodge 1954).

Other workers (Aitken 1962) using much narrower experimental areas had inconclusive results. Algal colonisation did not occur since limpets moved in from surrounding areas and grazed the algae as soon as they

settled. Constant removal of limpets from the experimental area and a "thinning out" of limpet numbers from nearby areas became necessary for any colonisation to take place. Eventually, algal colonisation did take place even on steeply sloping experimental areas. The algal growth was however less abundant than on gently sloping surfaces as used by Lodge (1948) and Jones (1946). Neither did the limpets move back in such great numbers.

Southward (1964) noted that re-colonisation and succession of algae would take place on artificially cleared or naturally cleared (as in a rock fall) rock surfaces. He introduced an important new concept into the relationship between limpets and algae: he stated that there was a cyclic relationship between the two types of organism where a temporary stabilisation can occur due to other factors, the most important being wave action. On wave-beaten shores where limpets were dominant over algae, the cycle was restarted by removing the limpets. Stability was finally re-established after five to seven years when the limpets removed the algae and were again dominant. On sheltered shores there were few limpets due to silt deposition and lack of water movement. Interference with the cycle here could lead only to the re-establishment of fucoid dominance over limpets. Southward also stated that other grazing organisms such as littorinids were involved.

Thompson (1979) agreed with Southward (1964) in stating

that the cyclic relationship between limpets and fucoids reaches a balance on the shore due to a temporary stabilisation of the cycle at a specific point. On exposed shores the cycle stops at a stage favourable to limpets and on sheltered shores at a stage favourable to fucoids. On undisturbed shores the cycle becomes stabilized and requires a definite event to re-start, e.g., limpet removal.

If the fucoids are removed deliberately it usually results in the rapid re-colonisation of the rock surface since fucoid spores establish themselves more quickly than limpet spat. In nature, poor limpet recruitment also starts off the cycle and triggers off algal growth. Once the fucoids are well established they create a favourable environment for the recruitment of limpet spat. Limpets in turn graze the fucoids, grow rapidly and eventually weaken and kill the fucoids: a cycle described by many other workers. Once the fucoids are removed limpet numbers decline due to lack of food and migration to other areas. This phenomenon was also observed by Southward and Southward (1978). Thompson concluded by describing the intertidal community as "a constantly shifting mosaic" of algae, limpets and barnacles. A very appropriate description in view of the close relationship between these types of organism.

Dayton (1971) in a series of experiments carried out on the Pacific coastline of the U.S.A. obtained results

similar to those of European workers as regards the re-colonisation of cleared rock areas. He used rather drastic techniques for clearing the rocks of fauna and flora by blasting or burning. This cleared the rocks of everything living, including long lived algal hold-fasts. Re-colonisation occurred on both types of treated surface but it took longer on the blasted areas. Dayton assumed that there was a weathering or leaching effect on the prepared surfaces which had to take place before any re-colonisation could occur. This timelag between clearing a rock surface of growth and re-colonisation with new growth, was also noted by Southward and Southward (1978) although it is denied by other workers (Connell 1972). Dayton noted that the usual algal succession on his experimental areas was diatoms, followed by red and green algae which were eventually replaced by fucoids. It was at least four years before the fucoids regained their previous dominance of 70% cover.

Dayton also compared re-colonisation and succession patterns on two distinct types of intertidal community, one Mytilus (mussel) dominated, the other fucoid dominated. If patches of Mytilus were removed, algae colonised the bare areas. A species of red alga Gigartina was the first colonist, being replaced by fucoids later. The Mytilus could not re-establish in large numbers due to intense predation by carnivorous molluscs (Thaids). If patches of Fucus were removed from a Fucus-dominated

community, the underlying algae such as Gigartina became dominant. The fucoids quickly regained dominance however and occupied 50% of the canopy within two years.

Dayton also stated that if algae alone are removed from an experimental area and the limpets left untouched the algae did not recover to previous levels. There was a very slow natural succession hampered by limpet grazing. If the limpets were removed and the algae left (presumably present in sparse quantities) a very rapid growth of algae occurred resulting in succession and climax within two years. Algal cover was also greater than in control areas where grazing continued. Dayton's observations thus confirm European findings.

He also stated that intertidal communities, no matter where they occur in the world, were controlled by the same factors namely:- numbers of competitive dominants, continuous physical disturbance e.g., wave action, and continuous biological disturbance e.g., grazing. He considered growing space to be a very important limiting factor with large numbers of species competing for this resource.

Dayton (1975) divided the algae colonising an intertidal area into three types. The largest plants formed a "canopy" which grew over and severely shaded smaller plants. The "obligate understories", e.g., Corallina spp.

grew under the canopy and were protected by them from wave action, desiccation and ultra-violet light. The last group were often the smallest and could be described as "fugitives" or the "weeds" of the community. They were often ephemeral and died back naturally after a few months. e.g., Ulva, Porphyra, diatoms etc. Some were however comparatively long-lived e.g., Gigartina.

Dayton believed that light and growing space were the most important factors limiting algal growth, light levels being the most critical. In one of his experiments he removed the large canopy algae and left the understory algae intact. Within a few months the understory layer had suffered from desiccation, wave action and an excess of ultra-violet light and had died back leaving areas of bare rock. This gave the "fugitives" growing space and they exploited the available space.

This process was not observed in nearby control areas where the canopy layer was left intact. He observed, however, that when a canopy plant in a control area died for natural reasons (because of wave action) a similar process occurred, the die-back of the understory allowing fugitive species to become established. Eventually in the experimental areas the canopy species became re-established and overshadowed both understory and fugitives. The canopy species resumed a dominant role, the understory recovered due to protection and presumably the fugitives died back, either naturally at

the end of an annual life cycle or as a result of lack of light.

Dayton also stated that optimal conditions for the recruitment of the canopy species varied. The large brown alga Hedophyllum was dominant forming thick zones at moderate levels of exposure. At high degrees of exposure, however, the alga was reduced to fugitive status despite growing strongly and showing good recruitment. The response of algal spores in different environmental conditions is believed to be an important factor in zonation. (Dayton 1975).

Dayton, like Southward (1964), observed that grazing pressure by herbivores was equal on all three types of algae. He stated that once the algae grew above a certain size they were relatively safe from attack by herbivores. He also believed that the fugitive species exerted a competitive influence although he had no evidence to support this view. He stated that the recruitment of algae depends largely on the successful settling of spores, a view supported by Connell (1972). Most algae produce spores and therefore recruit in the favourable summer period. Algae that produce spores in winter can, however, exploit bare patches of rock left exposed after the removal of adult plants due to storm damage. A lengthy sporeling phase makes recruitment uncertain but also means that the plant

is more likely to survive adverse conditions through dormancy. The recovery of canopy plants sometimes depends on the success of recruitment when there is no competition from fast-growing fugitive species.

Connell (1972) has made some interesting observations concerning the colonisation of bare rock surfaces leading to algal succession and finally a climax community. He considered the theory that certain species must precede others in the succession, because they modify the environment thus making it more suitable for the establishment of later colonists. Connell rejected this hypothesis and explained algal succession largely in terms of sporeling establishment. In his view, the fact that fucoids took longer to colonise bare rock areas than green algae was probably not because the greens "prepared" the rock surface in some way for the brown algae, but rather because fucoids have generally larger, less mobile spores than greens, which makes it more difficult for them to colonise quickly.

The disappearance of early colonists such as diatoms or green algae was thought to be due to a smothering effect by larger, later colonists. However, several of the early colonists are ephemeral by nature and tend to disappear anyway without shading or smothering. This was confirmed by Dayton (1975). Northcraft (1948) also noted that the green alga Ulva lobata increased and decreased its range seasonally. The bare rock areas

were not colonised immediately by other species, which implies a lack of competition. Dayton (1975), however, claims that competition is present between ephemeral algae.

Connell (1972) stated that most intertidal communities are made up largely of mature slow-growing individuals that do not have great powers of regeneration and are slow to colonise a new environment. If these slow-growing individuals are removed, the quicker growing "opportunist" species, with a higher reproductive rate move in and colonise the area. These opportunists are however always present to some extent and form part of the community.

Connell (1972) agreed with Dayton (1971) that an obligate understory population of algae exists which dies without the protection of the larger, mature plants. The structure of the intertidal community relies on the interaction of factors such as length of breeding season, mobility of spores and mature size. Connell believed that although the early colonists do modify the environment to some extent, they do not necessarily cause a predictable succession. He stated that it was quite likely that the dominant plants e.g., fucoids, would still colonise a habitat if the early opportunist species were removed as soon as they appeared. He also believed that herbivores such as limpets did not cause an ecological disturbance since they were part of the system and they were only

important when considering algal succession. This seems a strange concept since they change the environment profoundly for most intertidal algae by removing most algal growth. Connell then went on to state that grazing controlled all algal populations on the shore equally. This contradicts an earlier study by Southward (1964) where he claimed that limpets rejected the encrusting brown alga Ralfsia. Connell confirmed Dayton's (1971, 1975), observations that limpet removal begins a cycle of algal growth followed by an influx of limpets which result in the grazing and removal of algae, the same pattern occurring on both European and American shores.

Lewis and Bowman (1975) introduced another aspect to the make-up and control of intertidal communities based on studies of limpet settlement. They found that the level of algal settlement on the rock surface seemed to affect limpet spat settlement. At low levels of algae, spat settlement was more successful possibly due to the increased moisture level. At high algal densities however, the algal fronds may have had a screening or dislodging effect on the spat which prevented them from settling. The influence of fucoids on limpet settlement can be considerable when increased moisture levels enable limpets to settle higher up the shore than normal. When adult limpets were removed, fucoids eventually grew in the cleared areas.

Limpet spat therefore settled more successfully due to

increased moisture levels. The limpet growth rate was also higher on rock areas adjacent to stands of Fucus than on bare rock alone. This was probably due to increased food supplies. When Lewis and Bowman cleared a barnacle-dominated area of its limpets, fucoids grew and the barnacles declined, probably because of the sweeping effects of the fronds dislodging larvae. Limpets moved back into the area to graze the fucoids and there were larger numbers of limpets in this experimental area compared with control areas. This phenomenon was also noted by Southward and Southward (1978). Southward concluded that limpets contribute to the maintenance of constant biological conditions by limiting the establishment of fucoids and allowing the establishment of barnacles.

Southward and Southward (1978) published an interesting account of algal re-colonisation after the Torrey Canyon oil disaster. The oil spillage and subsequent treatment of affected areas by dispersants killed all plant and animal life in intertidal communities on parts of the Cornish coast. It provided an ideal opportunity to study plant and animal colonisation starting from bare rock.

The disaster occurred in early 1967 and by June Enteromorpha and Ulva had colonised the rock surface indicating the absence of grazers. Both algae showed rapid reproduction with peak spore production at

high tide. They undoubtedly fit into Daytons "opportunist" category of algae. By September 1967 Fucus vesiculosus and F. serratus had begun to colonise the cleared areas. It was observed that the greens such as Enteromorpha spp. always preceeded the brown algae in the succession. Southward believed that this could be due to increased shelter provided by the greens for the brown algae. (A theory disputed by Connell (1972)). It was also possible that the oil dispersants took time to disappear from the rock surface thereby allowing the brown algae to colonise. Eventually limpets migrated into or settled on the re-colonised areas and grazed down the algae.

Barnacles settled on the bare grazed areas and the rock surface began to revert back slowly to its pre-disaster condition. The limpets did not at first appear in sufficiently large numbers to affect the heavy algal growth to any appreciable extent. After 1969 limpet dominance of the re-colonised areas increased and the fucoids became weakened as a result of grazing and died or were swept away by wave action. As a result of grazing the shore became virtually bare of algae by 1975. The limpets were then forced to graze microscopic or encrusting algae. The animals formed huge limpet "fronts" advancing along the rock areas exploiting new sources of food. The areas cleared of algae became barnacle-dominated and by 1977 the re-colonised areas were white with large numbers of these animals. This relationship between fucoids, limpets and barnacles

was also observed by Lewis and Bowman (1975)

More recent observations have confirmed this triangular relationship between fucoids, barnacles and limpets, which may arise because of competition for primary space on the rock surface. Thompson (1980) removed limpets from a limpet and barnacle dominated area. A year later 47% of the experimental area was covered by Fucus vesiculosus sporelings and the area was dominated by fucoids and not by barnacles.

Southward also noted that the high density of fucoid plants on re-colonised areas produced large numbers of spores locally. This meant that colonisation of surrounding areas of rock was higher than usual due to the high availability of spores. A similar situation was also noted by Lodge (1948) and Thompson (1979). Southward observed that certain brown algae such as Ascophyllum nodosum are very slow growing, as also noted by Pyefinch (1943). The slow regrowth of this alga makes it more susceptible to grazing pressure and wave action. Re-colonisation of cleared areas to previously high levels of cover is very slow and sometimes does not occur at all.

To summarise, it is possible to make the following conclusions concerning limpet grazing and algal succession.

1. Limpets are generalist feeders which under certain circumstances are able to clear rock surfaces of almost all macro-scopic algal growth. They are more numerous on exposed shores (Jones 1946).

2. They probably have a cyclic relationship with algae where either one may be dominant over the other depending on the nature of the shore (Southward 1946).

3. The re-colonisation of a cleared rock surface by algal sporelings may only occur after a certain degree of "weathering" of the rock has taken place. Dayton (1971) and Southward and Southward (1978) agree with this whilst Connell (1972) does not. N.B. Weathering in this context means the physical and chemical changes brought about by colonising micro-organisms e.g., bacteria.

4. The pattern of algal succession on cleared rock areas is well established by both American, (Dayton 1971), (Connell 1972), and European, (Pyefinch 1943), (Lodge 1948), workers. The first colonists are almost always green "ephemeral" species followed by fucoid "dominant" species.

5. There is some evidence supplied by Dayton (1971) and Connell (1972), that there is intense competition between algae for growing space and light. This has resulted in a "two-storey" arrangement of algae, the "upper-storey" forming a canopy over the smaller "understorey" species.

6. There is also some evidence that a triangular relationship exists between limpets, algae and barnacles, these organisms being in direct competion for primary space on the rock surface. (Lewis and Bowman 1975, Thompson 1980).

In the present study sites were selected for limpet clearance on an exposed, rocky shore with suitable control areas nearby for comparison. A primary aim was to determine whether algal colonisation occurs on these sites in a similar way to that on more sheltered shores, since previous workers selected sheltered shores for observation.

The cyclic changes that are described by some authors (e.g., Lewis), which may confuse the results of a clearance experiment made it necessary to monitor not only the experimental areas but also control areas nearby in case the changes observed occurred independently of grazing.

Observations made in earlier studies were based mainly on the presence or absence of species. This study monitored the progress of change using quantitative methods rather than purely qualitative. This made it possible for accurate plans of each area to be drawn up for comparative purposes.

1.2 Limpet grazing and algal zonation

A second aim of this study was to study the effect of grazing by limpets on the vertical distribution of certain algae. For many years it was believed that physical factors such as tolerance to desiccation or wave action were responsible for the vertical distribution of algae on the shore and that the living populations of each zone were random aggregations of species all sharing the same tolerance to similar stress levels. It is now known that predation and biological interaction can affect both zonation and community structure. Algae in particular are affected by competition for space as well as tolerance to light and desiccation. Grazing by limpets reduces both algal and barnacle populations which affects community structure. Abiotic factors such as adverse weather conditions can also affect community structure by reducing the recruitment of spores and larvae.

Lodge (1948) supplied evidence for the influence of grazing on zonation when she showed that algae recolonising areas cleared of limpets do not form clear zones. Instead of clear-cut zones of Fucus spiralis, F. vesiculosus and Ascophyllum nodosum, the three species tended to grow together in the experimental strip without forming zones. She also observed that the brown A. nodosum influenced the vertical distribution

of another brown, F. spiralis, which normally grew higher up the shore than A. nodosum. However if the Ascophyllum plants were removed (for some reason) then F. spiralis grew quite readily in what was previously the Ascophyllum zone.

This interruption of the normal zonation of algae during re-colonisation was first observed by Pyefinch (1943). One of the areas which he selected for clearance of all fauna and flora was in the Ascophyllum nodosum zone (mid-shore zone alga).

However the dominant seaweed which eventually established itself in the cleared area was not A. nodosum but F. vesiculosus. It was suggested that the competitive balance between A. nodosum and F. vesiculosus was altered during the clearing of the area of it original fauna and flora: the lack of competition from A. nodosum apparently allowed F. vesiculosus sporelings to become established.

Pyefinch thus claimed that limpet grazing has a marked effect on algal zonation and was the first worker to suggest that grazing may indeed influence the competitive balance between algal species.

Recent studies have demonstrated that Ascophyllum is very slow to re-colonise cleared areas (Southward and Southward (1978). The conditions necessary for sporeling

establishment are also critical and may not be present every year. F. vesiculosus on the other hand has a rather wider exposure range than Ascophyllum and is a more efficient re-coloniser.

Pyefinch's claim that lack of limpet grazing allows one alga to increase its range at the expense of another may not therefore be correct. It is possible that the increase in range of the F. vesiculosus into what was the A. nodosum zone may be the result of more successful recruitment by F. vesiculosus spores.

A similar situation (where a marine grazer apparently controls the competitive balance of algae) was observed by Mann (1972) off the Canadian coast. Sea urchins (Echinus spp.) grazed extensively on a Laminaria species. Once the Laminaria had been removed as a result of the grazing activity of the sea urchins then another brown alga, Agarum cribosum, established itself in the cleared areas. A. cribosum was previously present only as a "fugitive" species. It appeared likely that the Laminaria competed with A. cribosum and limited part of its range. Once this limiting factor was removed the A. cribosum was free to extend its range.

Jones and Kain (1967) also observed that grazing by Echinus esculentus limited the range of Laminaria species themselves. The algae formed a zone offshore whilst

the sea urchins occupied an area between the Laminaria zone and the shore line (Low Water Mark). Once the sea urchins were removed from the area the Laminaria increased its range towards the shore. The grazing effect of the urchins therefore had a direct effect on the distribution and range of the Laminaria species. There is thus abundant evidence that grazing animals such as limpets and sea urchins appear to affect the vertical distribution of algae and the competitive balance between species.

Dayton (1971) observed that the distribution of plants and animals in his experimental areas was altered as a result of his experimentation whereas the control areas remained unaltered. He concluded that community structure on the shore was affected by numerous factors such as physical disturbance and competition for living space.

Dayton believed that there is strong competition between algae for light and growing space. Algal spores are able to settle on bare rock surfaces and on the surface of animals such as limpets and barnacles; the settlement area is due to chance. The rock surface itself is known as primary space and the limpets etc., as secondary space.

Competition for primary space is intense. Barnacles may grow and dislodge algal holdfasts thereby killing them or they may grow over and kill encrusting algae, such as

Phymatolithon spp. Dominant fast-growing algae may "squeeze out" smaller slow-growing species. During 1966 Dayton cleared an area of rocky shore of the sea-anemone, Anthopleura elegantissima from a very large aggregation of the animal. The usual succession pattern of diatoms and green algae was observed on the cleared area but there was little recovery by the anemone. Even by 1969 only a few anemonies had migrated into the cleared area, presumably because they were unable to compete with the faster growing algae. The results of this experiment indicated that the distribution of a fast-growing species, an alga in this case, can be extended at the expense of a slow-growing one such as a sea anemone. This could change zonation patterns. As a result of his studies Dayton thus confirmed that there were important biological factors controlling zonation as well as purely physical ones such as wave action. (this was also noted by Mann (1972).

An idea introduced by Connell (1972) was that the relative importance of physical and biotic factors in controlling zonation differed at different shore levels. He stated that the upper limit of any zone (particularly in the upper shore) was determined by physical factors such as increased desiccation, higher temperatures, stronger solar radiation or aspect. Inter-specific competition which is an important factor in zonation was believed to be most intense in the lower zones where conditions were more favourable for intertidal

organisms and least intense in the upper zones where conditions were less favourable. Connell believed that the upper limit of a zone could be moved upwards by increasing moisture levels, as noted by Lodge (1954) and Southward and Southward (1978). Thus the upper limit for a species on the shore appears to be determined by increased mortality as a result of extremes in the physical environment e.g., drought or low temperatures. Connell (1972). Heavy wave action can under certain circumstances raise the upper limit of a zone of living organisms. The wave splash wets the rock surface enabling the organisms to survive higher up the shore than they would normally. The upper limit of the small "under-storey" algae has been found to be raised through the indirect effect of larger algae which keeps the surface beneath them moist, shaded and cooler.

Connell (1972) believed that the lower limits of a zone cannot always be explained in terms of the physical aspects of the environment e.g., the continued sub-mergence of high level algae will not necessarily kill them. Intertidal algae often have abrupt lower limits at the boundaries of two zones. It was suggested by Southward (1958) and Lewis (1964) that this is due to competition. At lower tidal levels algae grow faster due to increased moisture levels and inter-specific competition is more intense. Grazing can affect the lower limit of an animal species although there is no direct evidence that grazing affects the lower limit of

any intertidal alga. Grazing can however affect the age structure of an algal population since limpets graze the younger plants leaving the older ones more or less intact.

Another aspect which may affect zonation is the size of the plant. Larger plants are more likely to be damaged by wave action than small ones, a view expressed by Lewis (1976). The size and mobility of algal spores is also a very important factor in determining zonation patterns and community structure. Some intertidal algae have large heavy spores which apparently are not carried very far from the parent plants. This phenomenon was observed by Burrows and Lodge (1950) and by Southward and Southward (1978). Both sets of workers discovered that the heaviest recruitment of fucoids was in a "down-stream" direction from the adult plants. Large algae with heavy, sweeping fronds may also prevent other species from colonising the rock surface and thereby change the community structure.

Aspect and steepness of slope are other factors which influence zonation and algal growth. South facing slopes receive more sun than North facing slopes and this often increases algal growth. It is also possible that steep slopes on the upper shore become drier and hotter, subjecting the algae growing on them to more stress. Steep vertical slopes are less moist than gently sloping surfaces due to increased drainage and

reduced solation. Large organisms protect smaller organisms growing or living beneath them. The smaller species will die back to their holdfasts if the large "canopy plants" are removed. This was observed by Dayton in 1975. Dayton also believed that competition existed between the large "canopy" species. He based his observations on the results of an experiment where a dominant "canopy" species was removed from an experimental area. The other co-dominant "canopy" species in this experimental area increased their range. Dayton was not able to prove however that the increase in range of the other dominants was due to the removal of the original dominant or due to the co-incidental disappearance of a large chiton species which grazed in the area. Dayton (1975) confirmed Connells (1972) work by stating that the upper limit of an intertidal species was determined largely by physical factors and the lower limit probably by biological factors, the biological factors being particularly important on the lower shore and in more sheltered areas.

Lewis (1976) also believed that zonation is maintained on the shore by the interaction of physical and biological forces, both being important. On exposed shores the submersion/emersion time is more influential than on sheltered fucoid-dominated shores, since presumably the fucoids protect underlying organisms from the effects of desiccation and light at low tide. Lewis believed that biological stability was greatest and community changes the

least likely to occur where physical conditions were harshest and species diversity was low. He inferred from this that zonation is maintained on exposed upper shores largely by physical factors. Lewis agreed with Connell (1972) that recruitment of spores or larvae is also important in determining zonation patterns and community structure. He showed that poor recruitment of limpet spat during cold weather led to fewer adult limpets settling on exposed shores. This in turn led to less grazing and more colonisation by fucoids. He agreed with Southward's (1964) observations that limpets and fucoids have a cyclic relationship.

Southward and Southward (1978) observed that as the bare rock areas left after the Torrey Canyon disaster were re-colonised, zonation patterns were altered slightly. The Laminaria digitata/L.hyperborea/Alaria zone was raised above its normal limit by 1.5 - 2 metres. These algae were found growing where previously (pre-disaster) only limpets and barnacles were to be found. Corallina officinalis and F. vesiculosus were also more abundant than usual in these areas. After three years the Laminaria had re-treated down to its usual level but a zone of Himanthalia elongata was still present at 1 metre above its normal level. The normal zonation pattern was not re-established until 1973 - 1974 when a peak of limpet numbers was observed. The shift in algal zonation was believed by Southward to be due to the absence of limpet grazing pressure. On such an exposed shore, he believed that

biological interaction i.e., limpet grazing was more important than physical factors such as desiccation in influencing zonation on the lower shore.

The reason why the lower shore algae such as Laminaria and Alaria settled so high up the shore in the first place is probably because their sporelings were protected from desiccation by a temporary "canopy" of fucoids and other algae. In pre-disaster conditions the rock surface would be populated only by barnacles and limpets which would offer the sporelings no protection and they would be grazed down. Corallina is definitely and "understorey" species and because it was protected by the growth of a fucoid "canopy", it grew more abundantly. The increase in range of F. vesiculosus can be explained by its relatively mobile spores which can quickly re-colonise a bare rock area. It increased its range due to lack of grazing. The return of the zones to more normal levels probably coincided with the return of the limpets in large numbers. They often damage holdfasts by their grazing activities and the entire plants were sometimes removed by winter storms.

Southward also observed an upward shift in the upper limit of other types of algal and animal zones because of increased shelter and moisture levels created by the fucoid "canopy", e.g., the Polychaete Annelid Spirorbis rupestris was found higher up the shore than normal and so were the encrusting algae Lithothamnion spp. As the limpets returned and grazed the fucoids moisture levels

declined and the Lithothamnion died; it was also grazed by limpets. Southward believed that the disturbance caused to the ecosystem by removing a grazing animal has two effects on zonation: desiccation is reduced due to algal growth and other more complex interactions take place between herbivores and algae.

Although Lewis and Southward both agree that a cyclic relationship is present between algae and limpets, they disagree as to the factors which maintain stability and zonation patterns on the shore. As previously stated Lewis believed that physical factors such as exposure were largely responsible for establishing and maintaining zonation patterns particularly on exposed shores.

Southward however, introduced a new factor which was the effect of herbivore grazing on zonation. He believed that biotic factors were just as important as physical ones in determining zonation patterns. The physical environment of the area of shore studied by Southward in the early '70's after the Torrey Canyon incident remained unchanged i.e., it was still an exposed shore. The algae re-colonising this area however, did not form quite the same zonation pattern as before despite unchanging physical conditions. Some biotic factors such as the absence of grazing had changed and this resulted in new zonation patterns emerging. This was a temporary state of affairs and within a few years the original zonation pattern had re-established itself.

It is probably true to say that both authors are correct to some extent. Physical factors such as desiccation and exposure probably determine the basic zonation patterns of any shore. Biotic factors such as grazing or inter-specific competition may determine zone boundaries within the general zonation pattern.

Studies carried out in recent years on the effect of grazing on algal zonation may be summarised as follows.

Vertical distribution is controlled by several factors:-

a) Physical factors such as desiccation and exposure may control the upper limit of most algal zones especially on upper or exposed shores. This view was shared by Southward (1958), Lewis (1964), Connell (1972) and Dayton (1975).

b) Biotic factors such as grazing or inter-specific competition may limit the lower edge of algal zones especially on lower or sheltered shores. Dayton (1975).

c) Factors such as spore-size (Lodge 1950 , and Southward 1978), may influence zonation patterns since the larger spores tend to settle on surfaces near the parent plants.

d) The size of the algae may also affect zonation since the smaller algae are more vulnerable to exposure

and therefore, found lower down the shore (Lewis, 1976).

e) Extreme physical conditions increase the stability of an intertidal community, the stability being broken only by the introduction of a new factor e.g., limpet removal (Lewis, 1976).

f) The presence or absence of herbivores may change zonation patterns. This was observed by Southward (1978) and Mann (1972).

g) Changes in the vertical distribution of algae after re-colonisation due to limpet removal are sometimes due to inter-specific differences between sporeling growth rates. Pyefinch (1943), Lodge (1954), and Southward and Southward (1978), all describe the above phenomenon.

The major areas of controversy are:-

(i) The importance of physical and biological factors and their effect on zonation.

(ii) The extent of algal inter-specific competition and its influence on zonation.

(iii) The possibility that generalist feeders such as limpets do not greatly influence algal zonation patterns.

In addition to the aims previously mentioned, this study aimed:-

1. To compare the vertical distribution of algae on the experimental areas with the vertical distribution of algae in control areas, using quantitative methods to determine whether any changes occur in the normal vertical distribution of algae due to the removal of a possible limiting factor, i.e., limpet grazing.

2. To re-examine the controversy as to whether grazing controls the upper limits of certain species (Southwards view as opposed to Connells).

2. DESCRIPTION OF THE AREA

Holy Island is a small rocky island off the West coast of Anglesey (see Fig 1). The West coast of Holy Island (Grid ref. SH243795) consists of several rocky headlands connected by small coves or beaches (see Fig 2). This part of Holy Island is subjected to severe weather during the winter months, whereas the Eastern coastline is comparatively sheltered.

Since it was proposed to study the recolonisation of algae on exposed shores the Western coastline was selected as a study area.

A small stretch of coastline between Porth y Pwll and Porth y Post was chosen (see Fig 3) since this area is easily accessible from the road and fairly safe to visit during the winter months. Five stations were selected in this area; all were situated on fairly smooth rock surfaces without too many cracks or fissures. A description of these stations is included.

2.1 Angle of slope of the five stations

This was estimated using standard surveying techniques (see Methods - Section 3.3).

Figure 1 - The British Isles showing the position of Holy Island

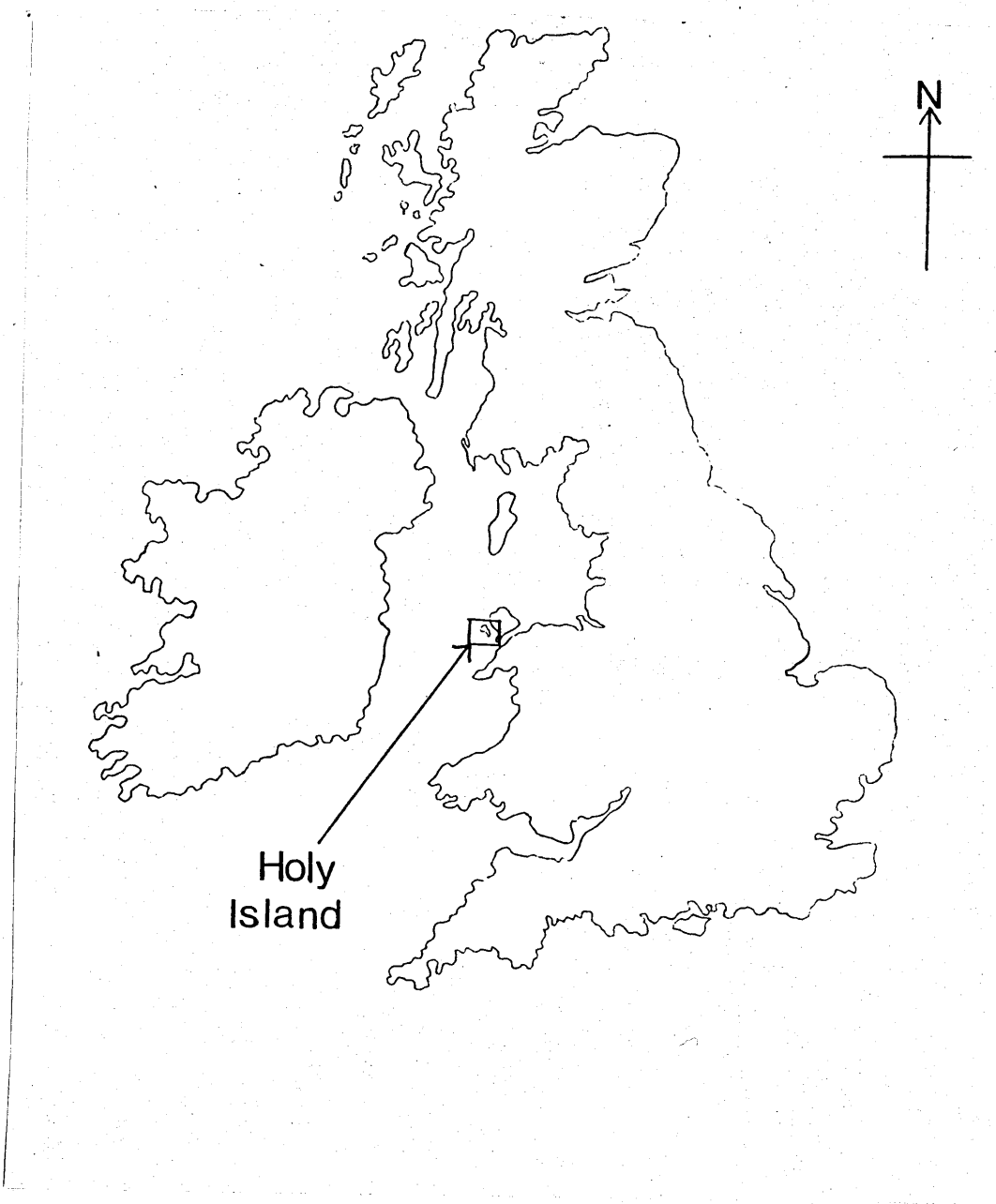


Figure 2 - Holy Island showing the position of the experimental area.

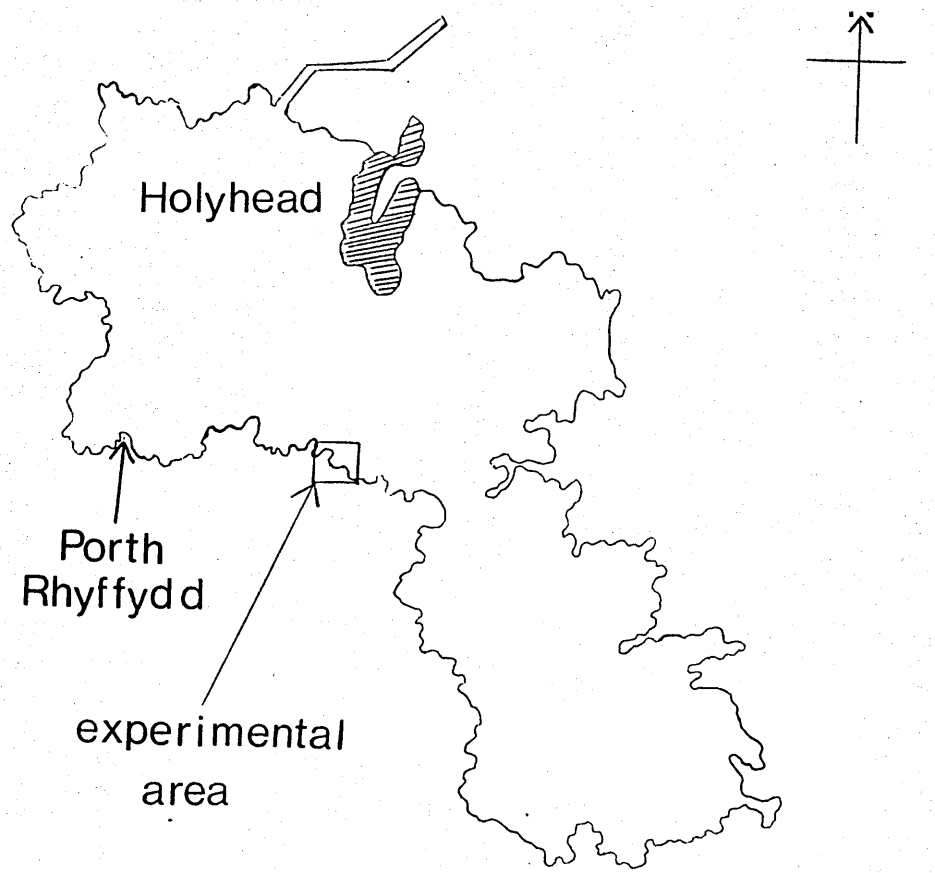
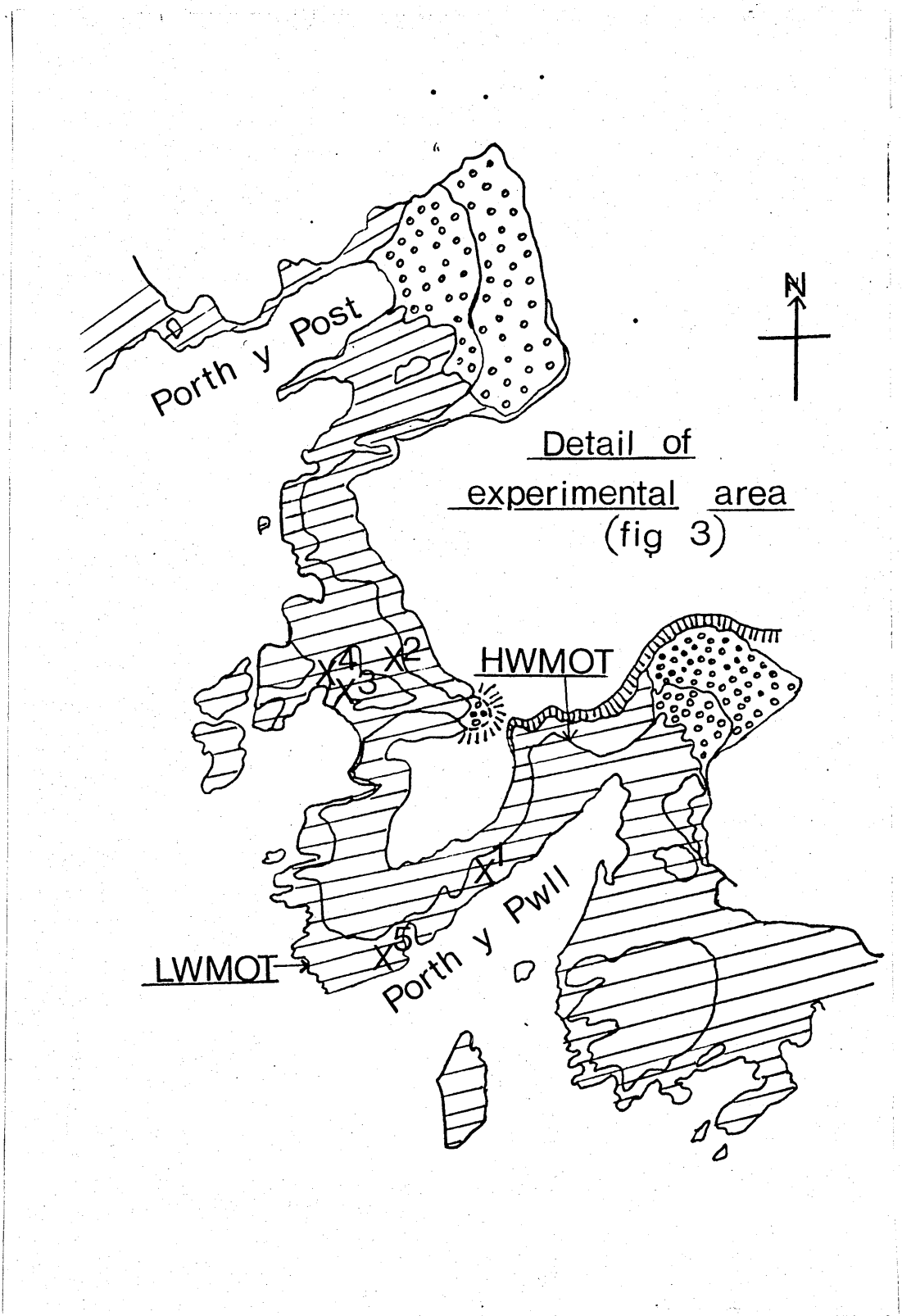
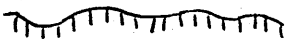


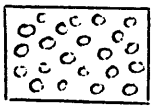
Figure 3 - Detail of Experimental area



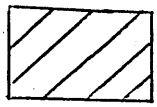
Key for Figure 3



cliffs



beach or cove



rocks covered by water at high tide

HWMOT — high water mark

LWMOT — low water mark

1 - 5 — five stations at which transects were taken

STATION	MAXIMUM SLOPE	MINIMUM SLOPE	AVERAGE SLOPE
1	46 degrees	11 degrees	13 degrees
2	-	-	14 degrees
3	-	-	50 degrees
4	-	-	21 degrees
5	41.5 degrees	8 degrees	35 degrees

The prevailing wind for this region is predominantly south-westerly, normally fresh in intensity and frequently reaching gale force 10. The rocks of this coastline belong to the New Harbour Group and are a Pre-Cambrian mica schist.

2.2 Description of five stations

STATION	DIRECTION OF SLOPE	DEGREE OF EXPOSURE	AMOUNT OF SHADING
1	South Facing	Semi-exposed	Shaded during late evening
2	Horizontal	Semi-exposed	Negligible
3	North Facing	Semi-exposed	Shaded for most of day
4	South Facing	Semi-exposed	Negligible
5	South Facing	Very exposed to exposed.	Negligible

2.3 Estimation of degree of exposure (based on Ballantine's 'Exposure scale for Rocky Shores'. (Ballantine 1961)

Definition of a semi-exposed shore:

This was based on the abundance of a few key plant and animal species:-

Pelvetia canaliculata - varies from occasional plants to common.

Fucus vesiculosus (bladderless form) - rare but larger plants than those normally found.

Fucus serratus - occasional.

'Lithothamnia' and Corallina spp - common in rock pools only.

Patella aspera - confined to pools.

P. vulgata - abundant and dominant.

Definition of a very exposed shore:

F. vesiculosus (bladderless form) - common.

P. aspera - abundant and dominant in infralittoral zone.

P. vulgata - dominant in upper mid-littoral zone

Gigartina stellata - common.

Station 5 also showed some of the characteristics of an exposed shore as follows:-

'Lithothamnia' and Corallina spp - common on rock surface.

Porphyra - absent in summer.

3. METHODS

3.1 General Methods

After selecting five stations for study, areas of rock on each station were marked out with pale grey paint (this colour was chosen to blend in with the surrounding rock). The paint had to be 'touched up' several times as it was removed by heavy wave action. These areas varied in size according to the area of smooth rock available at each station. Each area was two metres in width.

Dimensions of experimental areas

Station	Width	Length	Area
1	2 metres	8.5 metres	17 sq. metres
2	2 metres	2 metres	4 sq. metres
3	2 metres	3 metres	6 sq. metres
4	2 metres	2.5 metres	5 sq. metres
5	2 metres	5.5 metres	11 sq. metres

These rock areas were also photographed to indicate the distribution of algae already growing on the rock (photographs used for personal reference only and not included in present study).

In addition to photographs a scale drawing of each experimental area was made to indicate the area covered by each type of algae. Specimens of each alga were also removed and preserved for future reference.

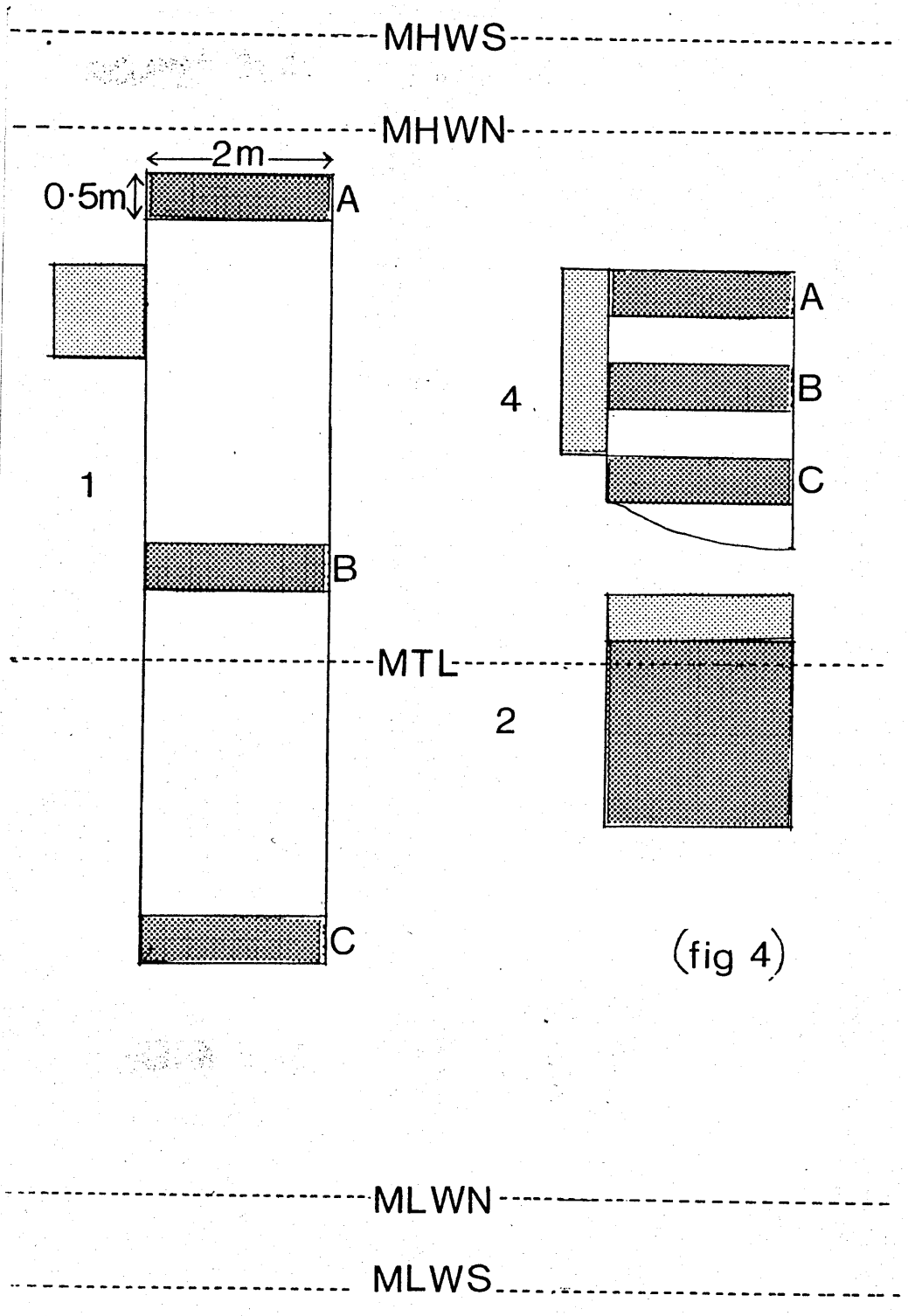
The experimental areas were cleared of limpets in the

late summer of 1974. The areas were then visited as often as possible to record any changes in the content and distribution of algal community. Any limpets that had migrated back into the experimental areas were removed since their grazing activities were found to check algal colonisation particularly in the early stages of growth.

As there was little visible change in the experimental areas for the first few months no quantitative studies were carried out at this time. Scrapings were however taken from the rock surfaces to discover whether or not any diatoms, blue-green algae or algal sporelings had begun to colonise the rock surface. In February 1975 there was sufficient algal growth to carry out quantitative studies using a quarter square metre iron quadrat. The percentage cover of each alga was measured by eye as accurately as possible. Quantitative studies were repeated at intervals until August 1978.

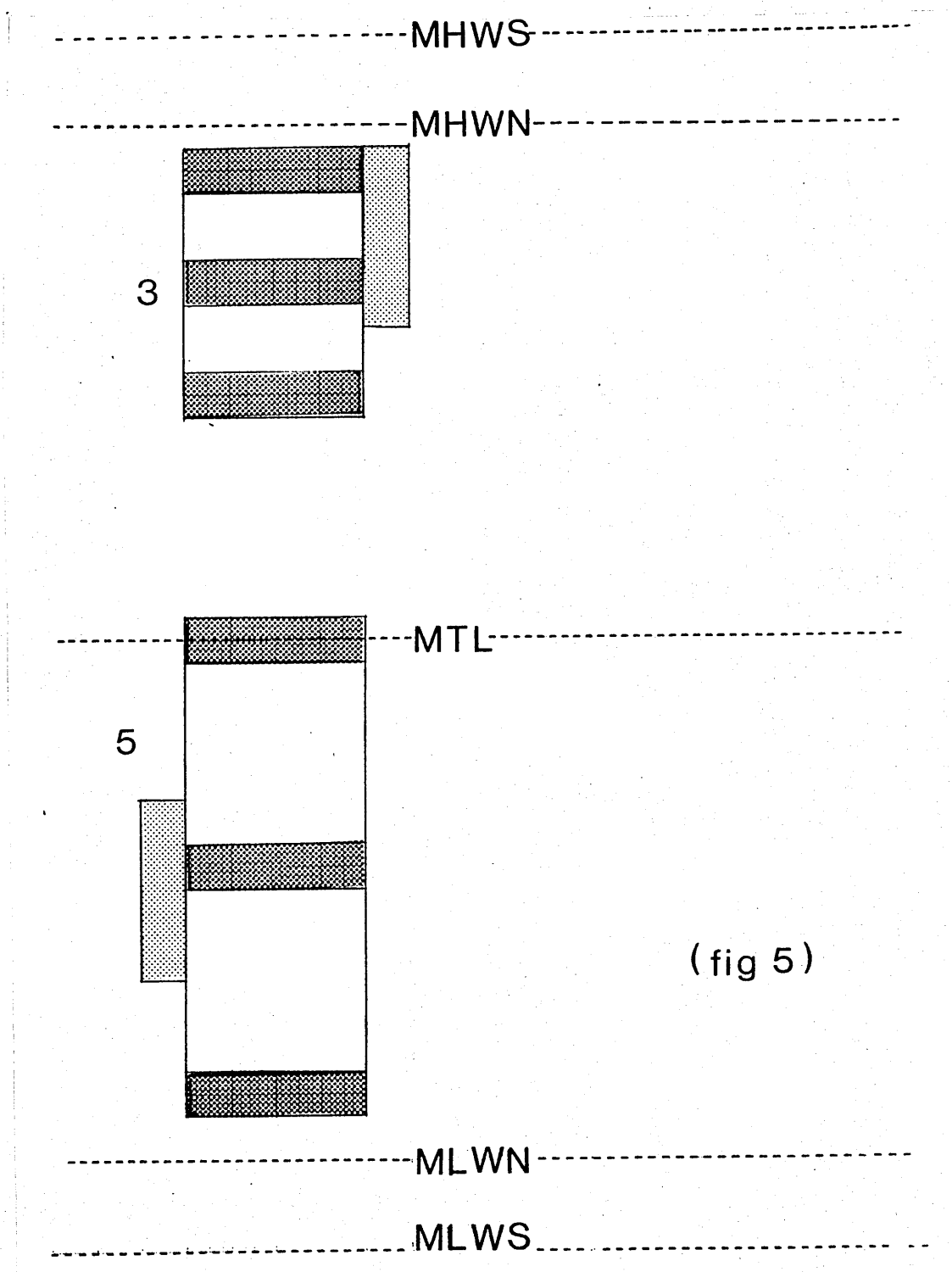
In addition to the five experimental areas, a control area of one square metre was selected at each station (see figures 4 and 5). These control areas were adjacent to the experimental areas so that the physical and biotic factors affecting both areas were as similar as possible. These were not cleared of limpets as it was intended to compare algal growth in these areas with growth in the experimental areas. The control areas were small as time did not permit any study of large areas as well as the experimental areas. Also, the experimental areas

Figure 4 - Diagram to show plan of Stations 1, 2 and 4 showing experimental and control areas



(fig 4)

Figure 5 - Diagram to show plan of Stations 3 and 5 showing experimental and control areas



(fig 5)

KEY FOR FIGURES 4 and 5

Control area

Experimental area - limpets retained for measuring and identification. (Areas A, B and C)

Experimental area - limpets cleared from this area also but not retained.

MHWS Mean High Water Spring

MHWN Mean High Water Neap

MTL Mid Tide Level

MLWN Mean Low Water Neap

MLWS Mean Low Water Spring

Scale of figures 4 and 5 - 1 centimetre equivalent to 1 metre

often filled most of the available smooth rock surface at each station. It was not thought necessary to have large control areas lying parallel to the whole experimental area since the control areas were meant to be a comparison giving evidence of change in the experimental area. Stations 2, 3 and 4 were situated north of Porth y Pwll whilst Stations 1 and 5 were situated in Porth y Pwll itself (see Figure 3).

3.2 Measurement of size and number of Limpets

The limpets were removed from the experimental areas and most of them thrown into the sea at least one hundred yards from the area from which they were removed. This was to prevent the limpets from migrating back to their 'homes' on the rock, (they have a well developed homing instinct). Limpets from certain parts of each experimental area were retained for counting, measuring and identification. (see Figures 4 and 5). These limpets were removed from three strips each one being one square metre in area from the top, middle and lower sections of each experimental area except site 2 when all removed limpets were measured. This was done to give some indication of the population density and distribution of limpets at each Station (for results see end of section).

The size of the limpets was estimated by measuring the length of the shell at its widest point. There were two species of Patella - P. vulgata and P. aspera. P. vulgata was more common higher up the rock surfaces but was replaced by P. aspera on rock surfaces near Mean Low Water Mark. This was more obvious in Station 5 which

was closer to Mean Low Water Mark than the other four experimental areas. It was fairly simple to distinguish between the two species of Patella since the foot of P. vulgata is a brownish-grey colour, whilst P. aspera has a bright orange foot.

Measurements of size and numbers of limpets per square metre of cleared area.

	A			B			C		
STAT.	No. of limpets removed	Min. shell size	Max. shell size	No. of limpets removed	Min. shell size	Max. shell size	No. of limpets removed	Min. shell size	Max shell size
		cm	cm		cm	cm		cm	cm
1.	20	2.1	4.0	108	1.1	4.0	137	1.1	4.0
2.	There were no A, B and C zones at this station as ALL the limpets were removed from the entire experimental area. These were all counted and measured. Total number of limpets removed = 458, minimum shell size = 0.6 cm maximum shell size = 5.5 cm								
3.	28	2.1	3.5	161	0.6	3.5	123	1.1	3.5
4.	35	0.5	3.5	119	0.5	3.5	117	0.5	4.0
5.	134	0.6	4.6	213	0.6	4.5	183	0.6	5.0

A = upper strip (one square metre in area) of experimental area.

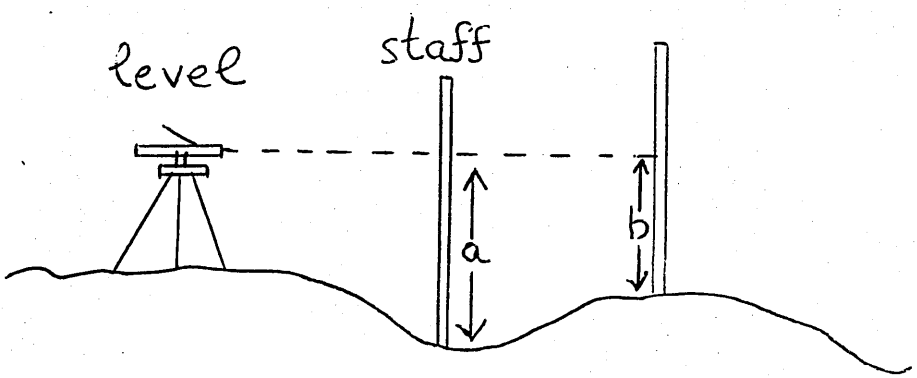
B = middle strip (one square metre in area) of experimental area.

C = lower strip (one square metre in area) of experimental area.

For the position of A, B and C (see figures 4 and 5) for positions on each station.

3.3 Levelling

In August 1975 each station was levelled to obtain the angle of slope by using a level and staff. An optical instrument, the level, was used to project a horizontal line of sight and from this the vertical distances down to the various points on the transect line were measured by observing, through the telescope, a graduated staff. This method was chosen as it was very accurate.



Height = a - b

The five stations were not all at the same height above sea level. Therefore the results from the levelling exercise had to be adjusted so that a direct comparison could be made of all five stations. Stations 2, 3 and 4 shared the same datum level as they were situated near to each other. There were different datum levels for Station 1 and for Station 2.

Calculations carried out for adjustments to levelling results

Sea level at Holyhead on 4th August 1975 at 1436 hours.
Adjustment for Porth Rhyffudd = minus 24 minutes.
(Porth Rhyffudd nearest reference point to Porth y Post according to Admiralty Tide Tables - for location of Porth Rhyffudd (see Fig 2).

Low Water at Porth Rhyffud = 1436 minus 24 minutes = 1412 hours.

Total height of water between High and Low Tide = 3 metres (4th August 1975)

At 1300 hours the tide was 0.08% of its total range above Low Water Mark = 300 x 0.08 = 24 cms.

Correction at 1400 hours for Stations 2, 3 and 4 = 0 cms

Correction at 1300 hours for Station 1 = minus 24 cms

Correction at 1340 hours for Station 5 = minus 3 cms

Correction to Mean Low Water Spring at Porth y Post

= minus 1.0 metres

Low Water at Holyhead on the 4th August 1975 at 1400 hours

= 1.7 metres above chart level

Mean Low Water Spring at Holyhead is 0.7 metres above chart datum.

Mean Low Water Spring at Porth Rhyfudd is therefore 0.7 - 0.1 = 0.6 metres above chart datum.

Low Water at 1400 on the 4th August 1975 at Porth Rhyfudd is 1.7 - 0.1 = 1.6 metres above chart datum.

Low Water at Porth Rhyfudd = 1.6 - 0.6 = 1.0 metre above chart datum.

Therefore the final adjustments for levelling results are as follows:-

Stations 2, 3 and 4 = minus 1 metre

Station 1, = minus 1.24 metres

Station 5, = minus 1.03 metres

Results of levelling

Station	Back Sight	Intermediate Sight	Fore Sight	Rise	Fall	Reduced Level	Remarks
1	2.89m					0m	Sea level 1300 h
		1.91m		0.98m		0.74m	Transect line 0 m
		2.08m			0.17m	0.57m	" " 1.5 m
		1.94m		0.14m		0.71m	" " 2.0 m
		1.51m		0.43m		1.14m	" " 5.2 m
		1.77m			0.26m	0.88m	" " 6.2 m
		1.23m		0.54m		1.42m	" " 7.4 m
			0.80m	0.43m		1.85m	" " 9.8 m
2	2.78m	2.13m			1.29m	1.34m	Bottom of transect
			2.67m		0.54m	1.84m	Top of transect
3	2.78m	3.14m			1.39m	0.83m	Bottom of transect
			0.84m	2.30m		3.13m	Top of transect
4			3.29m			0m	Level of sea 1400h
		2.10m		1.19m		1.19m	Bottom of transect
	2.78m	1.75m		1.03m		2.22m	Top of transect
5	2.46m					0m	Sea Level 1340h
		1.19m		1.27m		1.24m	Transect line 3.8m
		1.01m		0.18m		1.42m	Transect line 5.4m

Back sight - this is a sight from the level to the staff which is held at a station whose elevation is known.

Fore sight - this is a sight to an unknown station which will in turn be used when its reduced has been calculated as the next back sight.

Intermediate sight- this is a sight which is made to an unknown station which it is not intended to be used as a back sight.

The shore profiles determined by levelling are shown in figures 6 - 8.

Figure 6 - Shore Profiles at Stations 2, 3 and 4

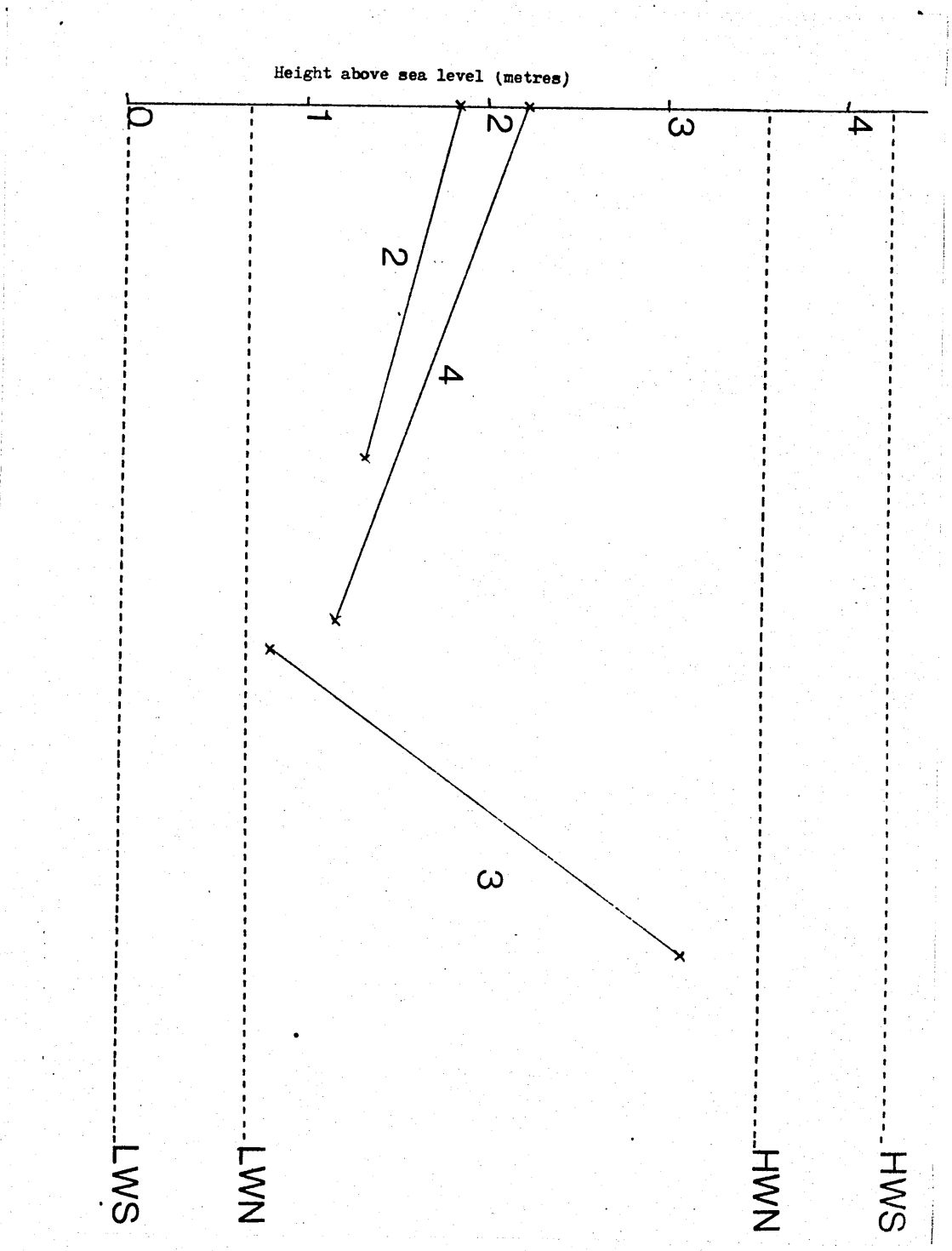


Figure 7 - Shore Profiles at Station 1

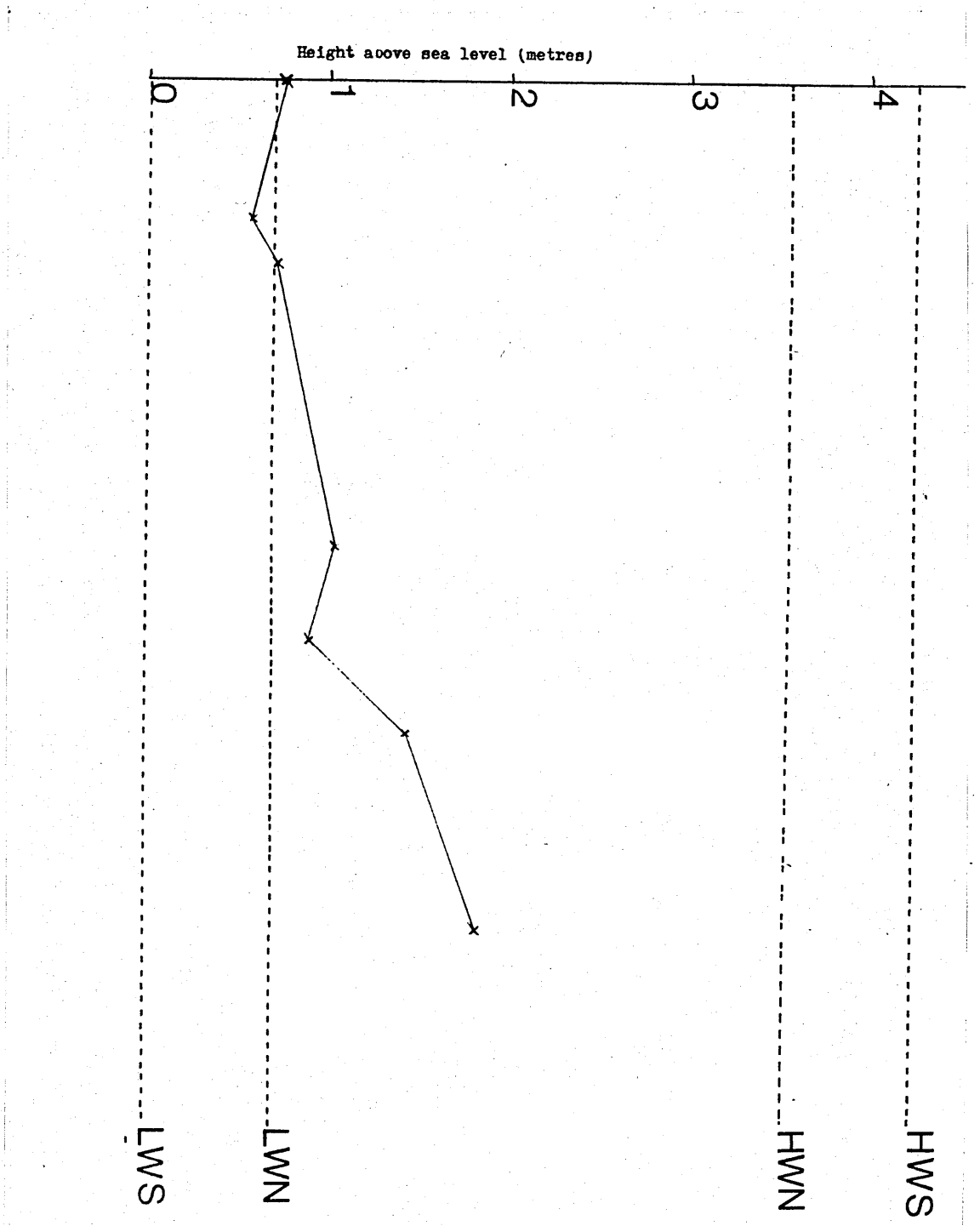
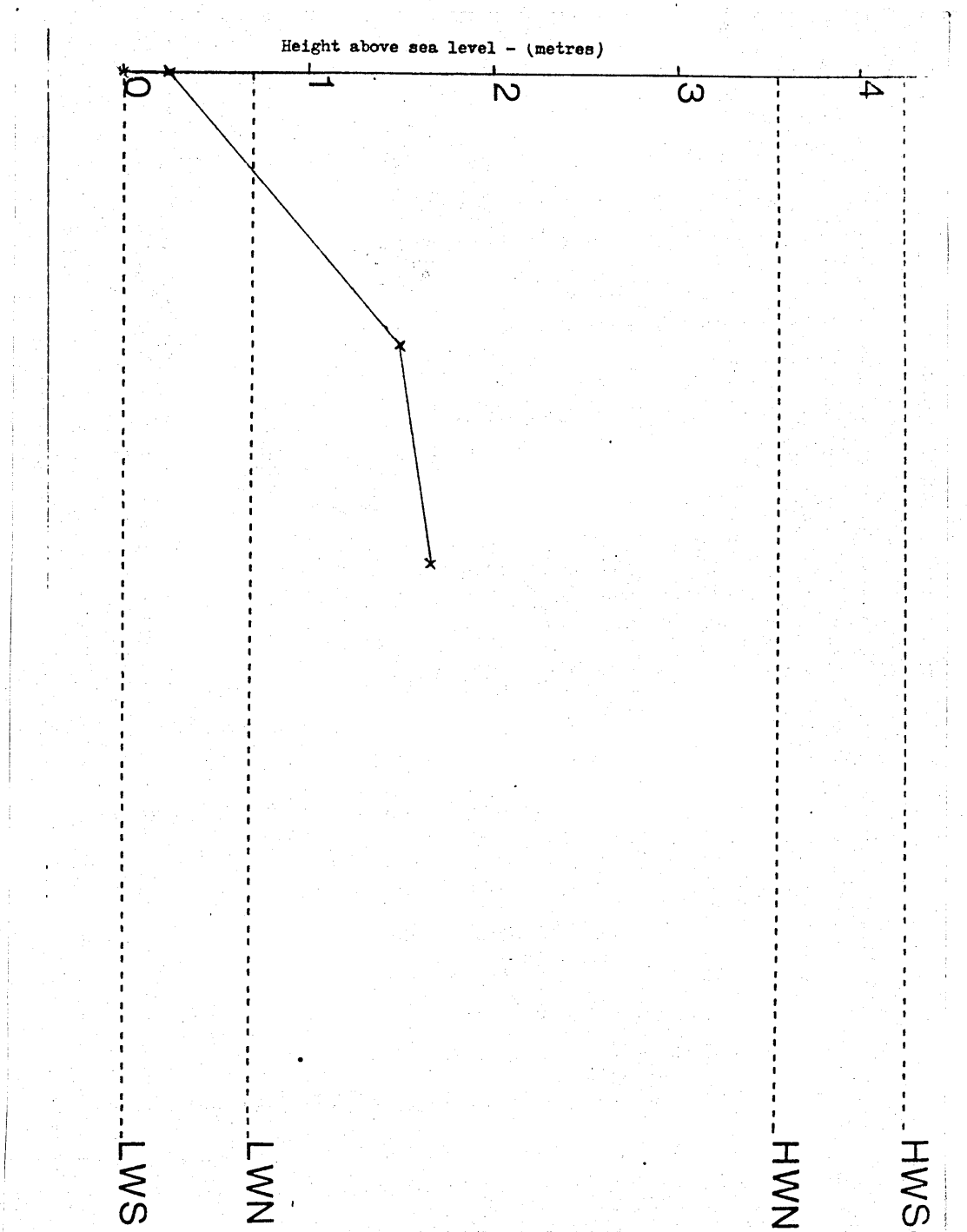


Figure 8 - Shore Profile at Station 5



3.4 Field work carried out on five experimental areas between August 1974 and August 1977

		Station 1	Station 2	Station 3	Station 4	Station 5
1974	Aug.	C Q	C Q	C Q	C Q	C Q
	Sept.	M	G M	G M	G M	-
	Oct.	M	-	M	M	-
	Nov.	-	M L	M	M	-
	Dec.	-	-	-	-	-
1975	Jan.	Q	-	-	-	-
	Feb.	L	Q L	G	Q L	Q
	Mch.	Q	Q	G	Q	Q
	Apr.	-	-	-	-	-
	May.	Q	Q	G	Q	Q
	Jne.	Q	Q L	G L	Q L	Q
	Jly.	Q L	Q L	G L	Q L	L
	Aug.	QQ	Q Q L	G	Q Q	Q Q
	Sept.	-	-	-	-	-
	Oct.	-	-	-	-	-
	Nov.	-	-	-	-	-
	Dec.	-	-	-	-	-
1976	Jan.	G	G	-	-	-
	Feb.	-	L	G L	G L	G
	Mch.	-	-	-	-	-
	Apr.	L	L Q	Q L	Q L	-
	May.	-	-	-	-	-
	Jne.	Q L	-	-	-	L
	Jly.	-	Q	Q	Q	Q
	Aug.	-	Q	-	-	-
	Sept.	-	L	Q L	Q L	-
	Oct.	Q L	Q L	Q	Q L	Q L
	Nov.	-	-	-	-	-
	Dec.	Q L	Q L	-	-	-

Plan of field work 1977

	Station 1	Station 2	Station 3	Station 4	Station 5
1977 Jan.	A L	-	-	-	-
Feb.	-	-	-	-	-
Mch.	-	-	-	-	-
Apr.	-	-	-	-	-
May.	-	-	-	-	-
Jne.	-	-	-	-	-
Jly.	-	-	-	-	-
Aug.	Q	Q	Q	Q	Q

Key for symbols used in field work plan

C Initial clearance of limpets from the five experimental areas (Aug 1974).

M Microscope studies of scrapings taken from the rock surfaces.

L Periodic clearing of limpets that migrated back to, or settled on the cleared experimental areas.

G General impressions of experimental areas, observations carried out either before there was sufficient algal growth to carry out quantitative studies or if weather and tidal conditions unfavourable for detailed study.

Q Quantitative studies carried out using a quadrat.

RESULTS

4.1 Observations 1974 - 1977

(including Tables 1 - 5 on percentage cover of algae at Stations 1 - 5).

Within a few weeks of the initial limpet clearance (August 1974), a fine brown film had developed on the surface of all five experimental areas. Microscopic examination revealed that this film consisted of diatoms, blue green algae, filamentous algae and bacteria. This film was not observed on the control areas.

Both experimental and control areas showed some evidence of seasonal growth of certain algae. Enteromorpha spp., Blidingia spp. and P. umbilicalis were abundant in the in the summer months. There was some evidence however that these algae were more abundant on experimental than on control areas although they occurred on both areas.

Station 1

Experimental area

Algal distribution on this experimental area was typical of a semi-exposed mid-shore (Ballantine 1961). Brown algae such as Fucus spiralis and F. vesiculosus (bladderless form) were present as small, scattered clumps on the rock surface. The smaller, red algae e.g., Laurencia pinnatifida and green Cladophora rupestris were confined to rock pools and crevices

(see Table 1). Limpets were present in large numbers e.g., 205 were removed from 1.5 square metres, indicating the high density of these animals. Their grazing activity had undoubtedly led to the large areas of bare rock present on this experimental area.

Twelve months after the initial limpet clearance, there was extensive algal growth over almost the whole of the experimental area (see Figure 10 and Table 1). The algae were mainly fucoids with extensive growth of Enteromorpha intestinalis (30% cover). The area covered by fucoids had increased enormously since the previous year. (F. vesiculosus increased its percentage cover from 11% to 52%). Presumably, limpet removal had also allowed E. intestinalis to become established. There was also a decrease in the percentage cover of Lithothamnion spp. from 11% to <1% during the first twelve months of the study, this may have been related to the increase in percentage cover of the canopy plants. Very little rock surface was visible compared with the previous year (percentage cover of bare rock had decreased from 64% to 22% by March 1975 - (see Table 1).

By June 1976 F. spiralis increased its range from 5% to 20% cover and F. vesiculosus had increased from 52% to 65% cover. They colonised almost the whole of the experimental area forming continuous sheets of alga covering the rock surface (see Figure 11). There had

been a considerable reduction in E. intestinalis which tends to be replaced by fucoids in the algal "succession". Red algae were never abundant on this Station and were still more or less confined to damp areas of the Station. There was some evidence however that red algal sporelings were beginning to colonise other areas such as under fucoids. The damp environment under the fucoids possibly made the rock surface a more suitable habitat for these delicate plants. Lithothamnion spp. increased its range from 11% to 20% cover from June to December 1976. This may have been due to the decrease in the fucoid percentage cover over this period, thus allowing the Lithothamnion spp. to increase its range. The fucoids were probably damaged and removed by winter storms and may have suffered during the dry summer of 1976. This increase in the percentage cover of Lithothamnion spp. was temporary possibly due to an increase in the fucoid canopy during 1977.

Between 1974 and 1977 the absence of limpet grazing allowed a general colonisation of the previously bare rock surface (see Figure 12). Algal zonation was observed at this Station with Pelvetia canaliculata growing in the first metre, F. spiralis growing in the first two metres and F. vesiculosus colonised the remaining six metres of the Station (see Figures 11 and 12).

Control Area

The control areas were not cleared of limpets and control area 1 was adjacent to the experimental area (see Figure 4). After twelve months there was little additional algal colonisation with only a few P. umbilicalis and F. vesiculosus plants present. By January 1977 about 20% of the rock surface was colonised by P. umbilicalis and F. vesiculosus (see Table 1). Eight months later about 40% of the control area was colonised mainly by F. vesiculosus and Enteromorpha spp. with large areas of rock left uncolonised.

The adjacent experimental area showed 100% algal cover by 1975 with virtually no part of the rock left uncolonised. F. vesiculosus grew vigorously in the experimental area compared with the plants in the control area. No observations were made on limpet numbers in the control areas, but it was assumed that they were normal for the area, i.e., high.

Station 2

Experimental area.

In 1974 the experimental area was sparsely covered by algae. There were a few scattered F. vesiculosus plants and several small colonies of Corallina officinalis, Cladophora rupestris and L. pinnatifida in crevices in

the rock (see Figure 16). This was again typical of a semi-exposed shore. The bareness of the rock seems to be due to the grazing activity of the many limpets which were removed from this area (over 100 limpets/m^2).

By August 1975 - 29% of the rock surface had been colonised by F. vesiculosus, (see Figure 17). One or two of the red algae showed a decrease in percentage cover e.g., L. pinnatifida was reduced from 8% to 2% possibly due to the smothering effect of fucoids. A few sporelings of Lomentaria articulata and Gigartina Stellata were beginning to colonise the damp rock surface beneath the growing fucoid canopy. This was not observed during 1974. E. intestinalis was also found on some areas not colonised by fucoids (see Table 2). There was a sharp increase in the percentage cover of Lithothamnion spp. from 0% to 59% in February 1975. It is possible that moister conditions during the winter months encouraged the increase in percentage cover of this alga.

Two years after limpet clearance the Station was almost completely covered by fucoids (the percentage cover of F. vesiculosus had increased from 29% to 87% in twelve months). Most of the increase occurred in the winter. The dominant plant was, of course, F. vesiculosus with a few F. serratus plants in the damper areas. Members of the Chlorophyceae and Rhodophyceae were less abundant than in 1975, probably due to the smothering

effect of the fucoid canopy. Those present included Chaetomorpha spp, C. rupestris and C. officinalis.

By August 1977 the Station was dominated by fucoids, a situation similar to that in Station 1. Fucoids were observed to follow plants such as E. intestinalis early in the succession. Zonation was not an obvious feature on this Station, the dominant plant being F. vesiculosus. However, there was very little slope to the rock and this may have been the main reason for lack of zonation. There was no F. spiralis present and the percentage cover of plants such as C. rupestris and C. officinalis remained more or less the same as in 1976 (see Figure 19).

Control area.

In 1975 the control area (adjacent to the experimental area - see Figure 4) contained scattered clumps of F. vesiculosus, C. rupestris, C. officinalis and others, the dominant alga was Lithothamnion spp. (percentage cover 21%). Twelve months later species composition had not altered appreciably. The percentage cover of fucoids had increased slightly in the boundary area between control and experimental area (see Figure 21). By 1977 the control area had altered only slightly with the fucoids continuing to grow in from the adjacent experimental area. Large areas of bare rock were still visible (62% in August 1977).

The experimental area became dominated by fucoids between 1974 and 1977. The extensive algal growth did not occur in the control area.

Station 3

Experimental area

This north facing site was devoid of macro-algae in 1974 and grazed heavily by large numbers of limpets (100 per m^2). By 1975 about 50% of the experimental area was colonised, mainly by fucoids and E. intestinalis. A few P. umbilicalis plants were also present (see Figure 23). Colonisation was not extensive on any part of the experimental area.

A year later 52% of the experimental area was colonised, mainly by fucoids which continued to extend their range. E. intestinalis, P. canaliculata and P. umbilicalis were also present but patchy in distribution (see Figure 24). There had been a reduction in the percentage cover of E. intestinalis since 1975 (from 40% to 6%) and an increase in the percentage cover of F. vesiculosus from 10% to 34% (see Table 3).

By 1977 there were large colonies of fucoids present, both F. spiralis and F. vesiculosus. Some of these colonies contained mature plants bearing reproductive bodies. E. intestinalis had been almost completely replaced by fucoids (see Figure 25). Growth was not

as extensive as in Station 1 or 2 possibly due to heavier wave action.

This was the only Station not to achieve 100% cover. This strongly indicated that the heavy wave action observed occasionally at this Station could be as important as limpet grazing in influencing algal growth.

As in Station 1, fucoid zonation was quite marked by the completion of the project. P. canaliculata was confined to the upper zone of the Station, F. spiralis to the middle zone and F. vesiculosus to the lower zone (see Figure 25).

Control area

The control area for Station 3 consisted of a narrow strip of rock adjacent to the experimental area (see Figure 5). Between 1974 and 1977 only one small colony of E. intestinalis and another of P. umbilicalis was found in this area (see Figure 26). Limpets were present in large numbers and the entire Station was subjected to heavy wave action. In contrast, however, the adjacent experimental area developed a dense fucoid "mat" between 1974 and 1977.

Station 4

Experimental area

This Station was a typical semi-exposed shore. The

sloping rock surface was very sparsely colonised mainly by F. vesiculosus, Enteromorpha spp., Lithothamnion spp. and C. officinalis (see Table 4). Most species were confined to rock pools (see Figure 27). The site was heavily grazed by large numbers of limpets (more than $90/m^2$).

By August 1975 the site was colonised by algae almost along the whole of its length. Until August 1975 it was thought that these were all F. vesiculosus plants, but on the appearance of reproductive structures it was obvious that the fucoids were a mixture of F. spiralis and F. vesiculosus. E. intestinalis colonised any rock areas not colonised by the fucoids. The members of the Rhodophyceae present had not increased their range (see Figure 28).

After two years the site was almost completely covered by a dense fucoid mat. This fucoid mat was approximately 50% F. spiralis and 50% F. vesiculosus (see Table 4). The zonation pattern of these two fucoids was complex and seemed to rely partly on height above sea level (F. spiralis is normally found higher up the shore than F. vesiculosus), and partly on the slope of the rock at Station 4. It was, therefore, possible to find F. vesiculosus growing above F. spiralis although it does not normally do so. Zonation was affected more on this site than on the other Stations. Few species were able to survive the shading effect of the fucoid

mass. E. intestinalis was present on the edge of the fucoids, C. officinalis and Chaetomorpha spp. were confined to a small rock pool. (see Figure 29).

By 1977 the Station was almost completely dominated by fucoids except for small areas of E. intestinalis. These colonies probably grew on bare patches left after the removal of some of the fucoids after heavy wave action. There was no change in the distribution of the other algae (see Figure 30).

The pattern of colonisation was similar to that found on the other three Stations. Enteromorpha spp. one of the first colonisers gradually being replaced by fucoids. There was, however, a slightly different zonation pattern on Station 4 as described above.

Control area

The control area for Station 4 was a narrow strip of rock adjacent to the experimental area (see Figure 4).

In June 1975 the only algae present were a few Fucus vesiculosus and Enteromorpha spp. plants as well as Lithothamnion spp. Twelve months later Enteromorpha spp. had increased their range possibly due to partial protection from desiccation by canopy plants growing in from the adjacent experimental area. P. umbilicalis was also present (see Figure 32). By 1977, the fucoids had

increased their range slightly probably growing in from the adjacent experimental area. There were still, however, large areas of rock visible (see Figure 33 and Table 4).

The experimental area showed an increasing domination by fucoids between 1974 and 1977, this was not observed in the control area since most of the fucoids observed in this area grew in from the experimental area.

Station 5

Experimental area

Out of the five Stations observed, this Station showed a larger and more varied range of algae. This was probably because of its exposed position (and therefore heavier wave action), and due to the fact that it was nearer low water level than the other five Stations. These two factors increase the moisture level on the rock surface and provide a more favourable habitat for colonisation. The dominant algae were F. vesiculosus (20% cover), C. officinalis (10% cover) and Lithothamnion spp. (50% cover). Algal distribution was patchy with bare rock areas populated by large numbers of limpets (average numbers 176/m^2).

Members of the Rhodophyceae were common on this Station, growing even on the exposed rock (see Table 5). They could not have survived in this situation on the other four Stations due to desiccation (see Figure 34 and Table 5 for algal distribution).

A year after clearance F. vesiculosus had increased its range until it had colonised about 37% of the Station. E. intestinalis although present in small quantities was never an important species in the early stages of colonisation as it was, for example, in Station 1. Members of the Rhodophyceae, e.g., Palmaria palmata (mainly epiphytic on F. vesiculosus), G. stellata and L. pinnatifida, had increased their range slightly probably as a result of increased shelter and humidity due to the growth of larger algae (see Figure 35). There was a sharp decline in the percentage cover of Lithothamnion spp. from 50% to 6% between August 1974 to June 1976. This could have been related to the increase in percentage cover of canopy species.

In 1976, F. vesiculosus continued to increase its range until it had colonised half the experimental area (56% cover). E. intestinalis was not abundant and was confined to areas such as rock pools or any areas not colonised by F. vesiculosus. G. stellata continued to increase its range under a protective algal canopy (see Figure 36). The percentage cover of Himanthalia elongata increased from 4% in 1975 to 15% in 1976 (see Table 5). This may have been due to increasing humidity and protection provided by increasing fucoid cover. As fucoid cover decreased (from 56% in 1976 to 43% in 1977) the percentage cover of the H. elongata also went down.

After three years, the Station was more or less covered

by algae. F. vesiculosus was the dominant alga although showing signs of storm damage or possibly age by this time (the fucoid plants live for about three years). E. intestinalis had increased its range from 4% in 1976 to 30% in 1977. This could be because the Enteromorpha spp. was colonising bare spaces left by the removal of fucoids after winter storms. Members of the Rhodophyceae such as G. stellata and L. pinnatifida flourished. The increase in range of some of the members of the Rhodophyceae was difficult to estimate because of their position under larger algae. (see Figure 37).

Zonation appeared to be normal at this Station with no mixing of zones. There was only one fucoid present, F. vesiculosus. This was replaced by H. elongata in the lower zone of the experimental area (see Figure 37). Zonation also occurred amongst members of the Rhodophyceae although one or two species were found throughout the experimental area e.g., L. pinnatifida (see Figure 37).

Control area

The control area was a narrow strip of rock adjacent to the experimental area (see Figure 5). In 1975 the area was sparsely colonised by scattered clumps of F. vesiculosus, E. intestinalis and G. stellata (see Figure 38).

There was 81% bare rock visible in the control area in August 1974 compared with only 6% bare rock visible in the experimental area. This could be explained by the 50% cover by Lithothamnion spp. on the experimental area. Lithothamnion spp. was absent from the control area but there was no obvious explanation for this phenomenon.

In October 1976 the percentage cover of F. vesiculosus increased from 12% in 1975 to 46% in 1970. Most of the increase was probably due to fucoids growing in from the adjacent experimental area between June and October 1976. There had been very little change in the range and distribution of other species. This trend continued in 1977 when 42% of the control area was covered by F. vesiculosus much of it caused by the growth of algal fronds from the adjacent experimental area (see Figure 40).

The experimental area showed an increase in algal cover and range between 1974 and 1977; this was observed to a much lesser extent in the control area. There was more algal growth in this particular control area than in the other four control areas. The "ground flora" of small Rhodophyceae plants, prominent in the experimental area of Station 5 was largely lacking in the control area. This may have been due to more limpet grazing or less shelter from desiccation provided by the fucoids of the experimental area.

Limpets do have catholic tastes whilst grazing but tend to avoid the harder, less digestible algae such as C. officinalis. (Southward 1964).

TABLE 1 - Percentage cover of algae at Station 1.

Algae	Experimental area						Control area		
	Aug 1974	Mch 1975	Aug 1975	Jun 1976	Dec 1976	Jly 1977	Feb 1975	Jan 1977	Aug 1977
Chlorophyceae									
Chaetomorpha spp.	-	-	<1	<1	-	-			
Cladophora rupestris	<1	-	<1	<1	<1	-			
Enteromorpha spp.	<1	<1	30	4	<1	9	-	-	9
Ulva lactuca	<1	<1	-	-	<1	-			
Phaeophyceae									
Fucus serratus	<1	<1	<1	<1	<1	<1			
F. spiralis	4	2	5	20	13	9			
F. vesiculosus	11	11	52	65	55	72	1	10	29
Leathesia difformis	-	-	<1	<1	-	-			
Pelvetia canaliculata	<1	-	<1	<1	<1	<1	-	<1	-
Rhodophyceae									
Callithamnion tetragonum	-	<1	-	-	-	-			
Ceramium spp.	<1	-	<1	<1	-	<1			
Corallina officinalis	<1	<1	<1	<1	<1	<1			
Dumontia incrassata	-	<1	-	-	-	-			
Gelidium corneum	-	<1	-	-	-	-			
Gigartina stellata	-	<1	<1	<1	<1	<1			
Laurencia pinnatifida	1	<1	1	1	1	1			
Lithothamnion spp.	11	5	<1	<1	20	-	<1	-	-
Lomentaria articulata	<1	<1	<1	<1	<1	<1			
Palmaria palmata	<1	<1	<1	<1	<1	-			
Polysiphonia spp.	-	<1	-	-	-	-			
Porphyra umbilicalis	-	4	3	<1	3	<1	<1	10	2
Lichnea pigmaea (lichen)		-	-	-	-	-	<1	<1	<1
Diatomaceous (slime)	-	38	-	-	-	-			
Bare rock	64	22	0	0	0	2	96	78	59

TABLE 2 - Percentage cover of algae at Station 2.

Algae	Experimental area							Control area					
	Aug 1974	Feb 1975	Aug 1975	Apr 1976	Oct 1976	Dec 1976	Aug 1977	Feb 1975	Aug 1975	Apr 1976	Jly 1976	Dec 1976	Aug 1977
Chlorophyceae													
Chaetomorpha spp.	-	-	1	<1	-	-	<1	-	<1	3	1	-	1
Cladophora rupestris	5	-	1	1	1	1	1	1	1	2	6	<1	<1
Enteromorpha spp.	-	-	11	-	-	-	<1	-	9	<1	2	-	7
Ulva lactuca	-	-	<1	<1	<1	-	-	<1	-	<1	-	-	-
Phaeophyceae													
Fucus serratus	-	-	-	-	4	3	-						
F. vesiculosus	5	22	29	75	87	91	90	<1	1	2	14	31	25
Himanthalia elongata	-	<1	-	-	-	-	-						
Leathesia difformis	<1	-	<1	-	-	-	-	-	1	-	1	-	1
Rhodophyceae													
Callithamnion tetragonum	-	<1	-	-	-	-	-						
Ceramium spp.	-	-	<1	-	-	-	-						
Chondrus crispus	-	-	<1	-	-	-	-						
Corallina officinalis	1	5	<1	1	<1	1	<1	2	1	1	-	1	<1
Dumontia incrassata	-	-	-	<1	-	-	-	<1	-	<1	-	-	-
Gelidium corneum	<1	-	<1	1	<1	<1	-	1	<1	<1	-	2	<1
Gigartina stellata	-	<1	-	-	<1	<1	<1	<1	-	-	-	-	-
Laurencia pinnatifida	8	<1	2	5	1	1	1	3	1	1	-	3	<1
Lithothamnion spp.	-	59	<1	3	1	4	-	21	-	10	-	27	-
Lomentaria articulata	-	<1	-	-	-	-	-	<1	-	-	-	-	-
Palmaria palmata	-	3	-	-	-	-	-						
Polysiphonia spp.	-	<1	-	<1	-	-	<1	-	-	-	<1	-	-
Pterosiphonia thuyoides	-	<1	-	-	-	-	-						
Bare rock	79	4	49	10	1	0	3	67	84	77	75	35	62

TABLE 3 - Percentage cover of algae at Station 3.

Algae	Experimental area						Control area				
	Aug 1974	Feb 1975	Aug 1975	Apr 1976	Sept 1976	Aug 1977	Feb 1975	Aug 1975	Feb 1976	Jly 1976	Aug 1977
Chlorophyceae											
Enteromorpha spp.	-	-	40	16	6	1	-	-	-	1	-
Phaeophyceae											
Fucus spiralis	-	-	-	<1	4	12					
F. vesiculosus	-	-	10	12	34	38					
Pelvetia canaliculata	-	-	-	<1	<1	2					
Rhodophyceae											
Porphyra umbilicalis	-	1	1	22	2	1	-	-	1	-	-
Bare rock	100	99	49	48	53	46	100	100	99	99	100

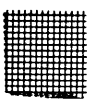
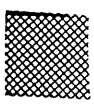
TABLE 4 - Percentage cover of algae at Station 4.

Algae	Experimental area						Control area				
	Aug 1974	Mch 1975	Aug 1975	Apr 1976	Oct 1976	Aug 1977	Feb 1975	Jun 1975	Apr 1976	Jly 1976	Aug 1977
Chlorophyceae											
Chaetomorpha spp.	-	-	-	-	-	<1					
Enteromorpha spp.	6	<1	11	8	-	13	-	<1	10	12	<1
Ulva lactuca	-	-	<1	<1	-	-					
Phaeophyceae											
Ectocarpus spp.	<1	-	-	<1	-	-					
Fucus spiralis	-	-	16	40	+	36	-	-	-	2	-
				F. vesiculosus							
F. vesiculosus	4	31	39	38	77	43	<1	<1	6	2	25
Rhodophyceae											
Bangia spp.	-	<1	-	-	-	-					
Ceramium spp.	-	-	<1	<1	-	<1					
Corallina officinalis	2	<1	<1	<1	<1	<1					
Dumontia incrassata	-	-	-	<1	-	-					
Laurencia pinnatifida	-	-	<1	<1	<1	<1	<1	-	-	-	-
Lithothamnion spp.	6	-	2	4	3	-	2	2	<1	-	-
Palmaria palmata	-	-	-	<1	-	-					
Polysiphonia spp.	-	-	-	<1	-	-					
Porphyra umbilicalis	<1	<1	<1	<1	<1	<1	-	-	<1	3	<1
Bare rock	80	65	27	1	17	3	96	96	82	81	73

TABLE 5 - Percentage cover of algae at Station 5.

Algae	Experimental area						Control area			
	Aug 1974	Mch 1975	Aug 1975	Jne 1976	Jne 1977	Aug 1977	Aug 1975	Jly 1976	Oct 1976	Aug 1977
Chlorophyceae										
Chaetomorpha spp.	<1	<1	<1	2	<1	<1	<1	-	-	1
Cladophora rupestris	<1	<1	<1	-	-	<1				
Enteromorpha spp.	<1	<1	<1	4	9	30	<1	-	-	<1
Ulva lactuca	-	-	<1	<1	<1	-				
Phaeophyceae										
Alaria esculenta	-	-	-	<1	<1	-				
Fucus vesiculosus	20	31	37	56	45	43	12	12	45	42
Himanthalia elongata	1	<1	4	15	3	4	-	-	-	<1
Leathesia difformis	-	-	<1	-	-	-				
Rhodophyceae										
Apoglossum ruscifolium	-	-	<1	<1	<1	<1				
Callithamnion tetragonum	<1	1	<1	1	<1	1				
Ceramium spp.	<1	1	<1	<1	<1	<1				
Corallina officinalis	10	6	4	4	4	4	1	<1	<1	<1
Gigartina stellata	2	1	4	9	7	7	<1	<1	-	2
Laurencia pinnatifida	2	1	4	3	4	5	<1	<1	<1	-
Lithothamnion spp	50	30	9	6	-	-				
Lomentaria articulata	-	-	<1	<1	<1	<1	<1	-	-	-
Nemalion helminthoides	-	-	-	-	<1	-				
Palmaria palmata	1	1	1	<1	4	6	<1	-	-	-
Polysiphonia spp.	1	<1	<1	<1	<1	<1	-	-	-	<1
Porphyra umbilicalis	<1	<1	<1	<1	3	<1	-	-	-	<1
Pterosiphonia thuyoides	<1	<1	<1	<1	<1	<1				
Bare rock	6	21	25	0	11	0	81	85	53	50

4.1.1 Key for symbols used to illustrate algae in figures 9 - 40 incl.

	Fucus spiralis	Lithothamnion spp.	
	Fucus vesiculosus	Gigartina stellata	g
	Laurencia pinnatifida	Callithamnium tetragonum	X Z
	Corallina officinalis	Polysiphonia spp.	y
	Enteromorpha spp.	Pterosiphonia thuyoides	t
C	Ceramium shuttleworthium	Chaetomorpha spp.	
r	Palmaria palmata	Himanthalia elongata	o
S	Fucus serratus	Lomentaria articulata	L
	Cladophora rupestris	Ulva lactuca	l
	Gelidium hornum	Porphyra umbilicalis	u
c	Pelvetia canaliculata	Leathesia difformis	d
n	Nemalion helminthoides	Lichnea pigmaea	i
	N.B.	Dumontia incrassata	m

All specific names cited here are in accordance with Parke and Dixon's "Check List of British Marine Algae - 3rd Revision" (1976) and the Plymouth Marine Fauna (1963).

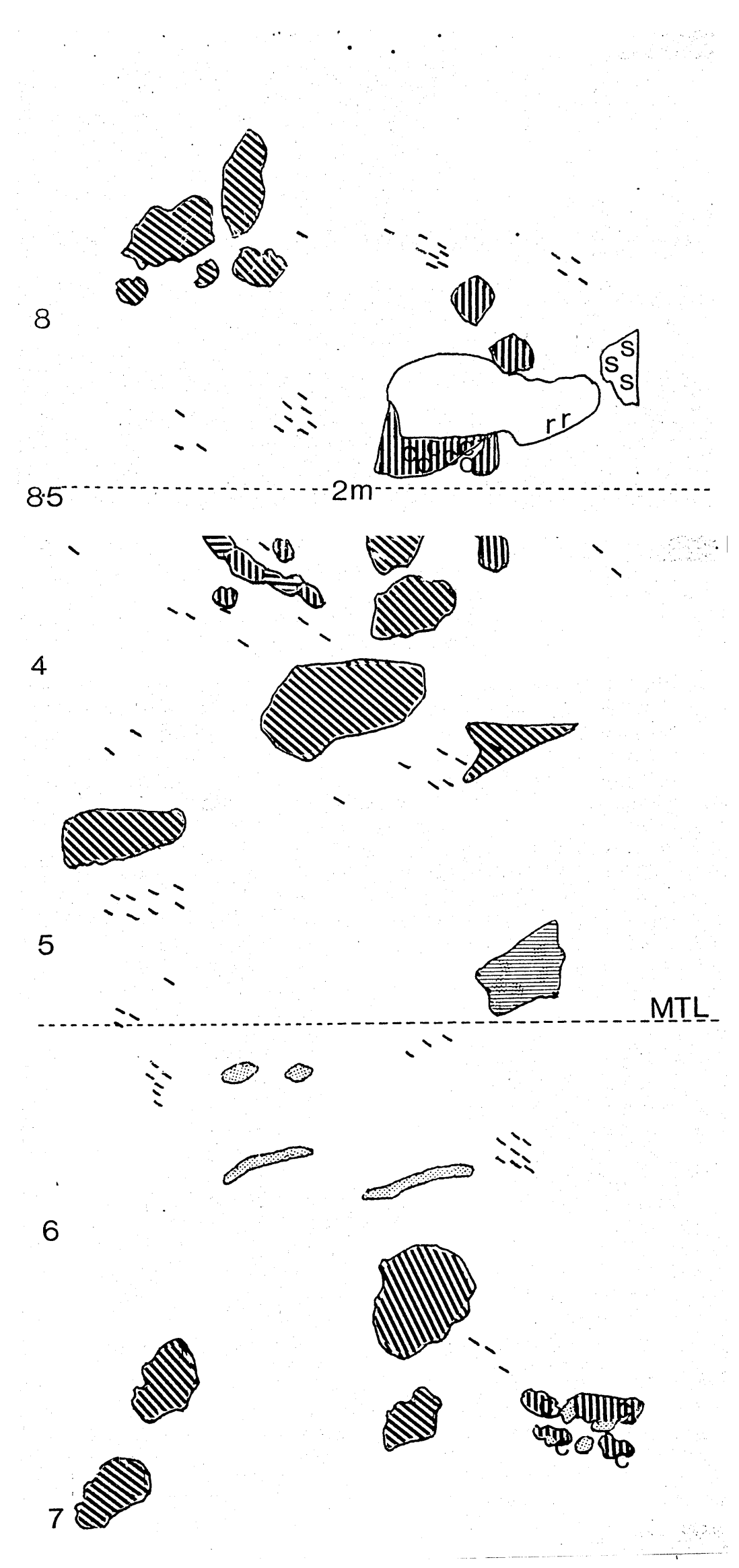

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Figure 9 - Station 1 - Distribution of algae August 1974

(partly diagrammatic)

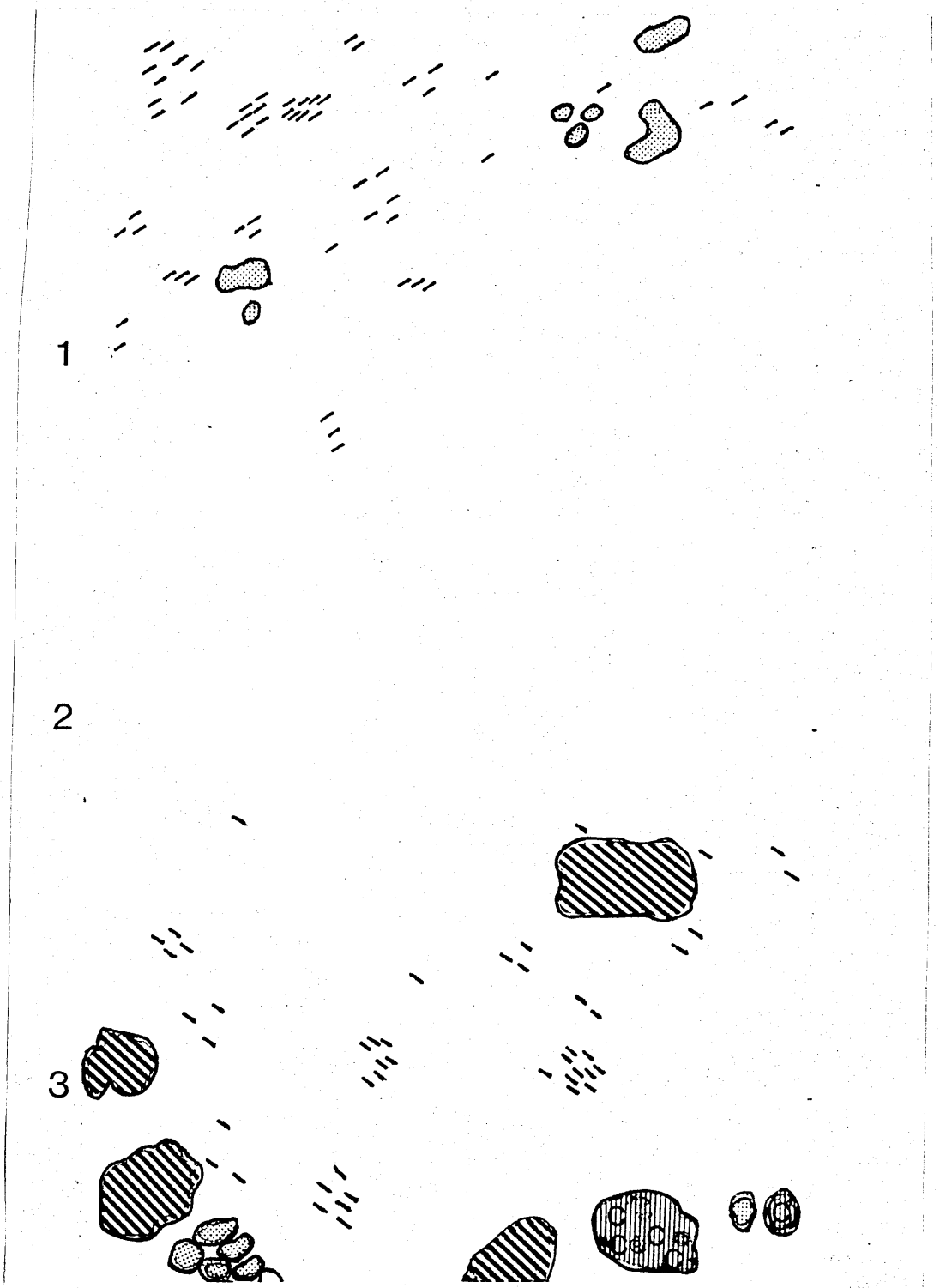

Figure 10 - Station 1 - Distribution of algae August 1975 (partly diagrammatic)

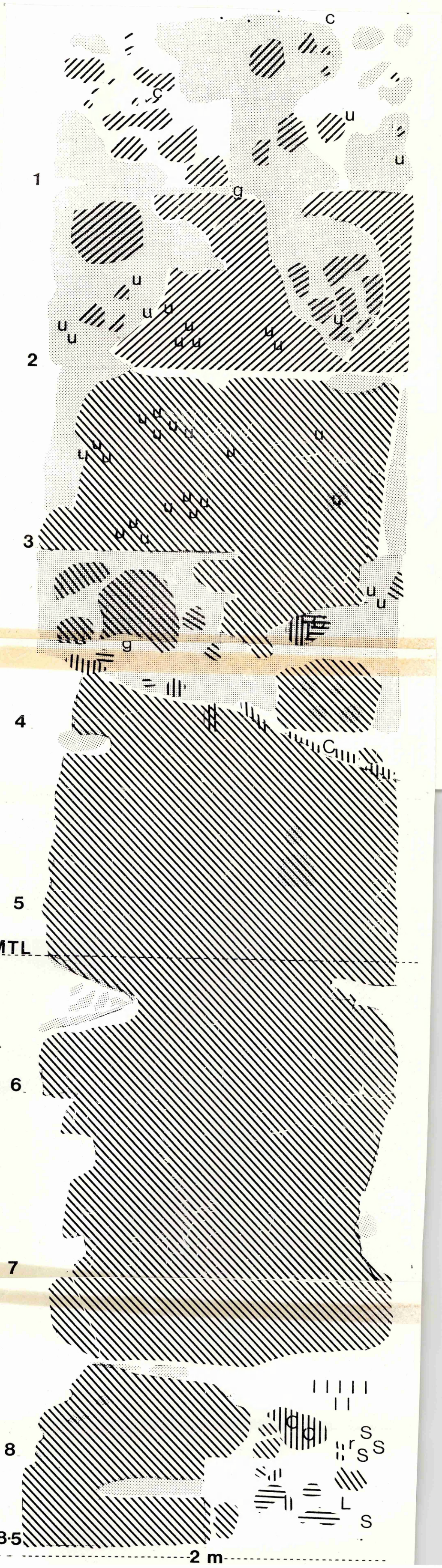
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Figure 11 - Station 1 - Distribution of algae August 1976

(partly diagrammatic)

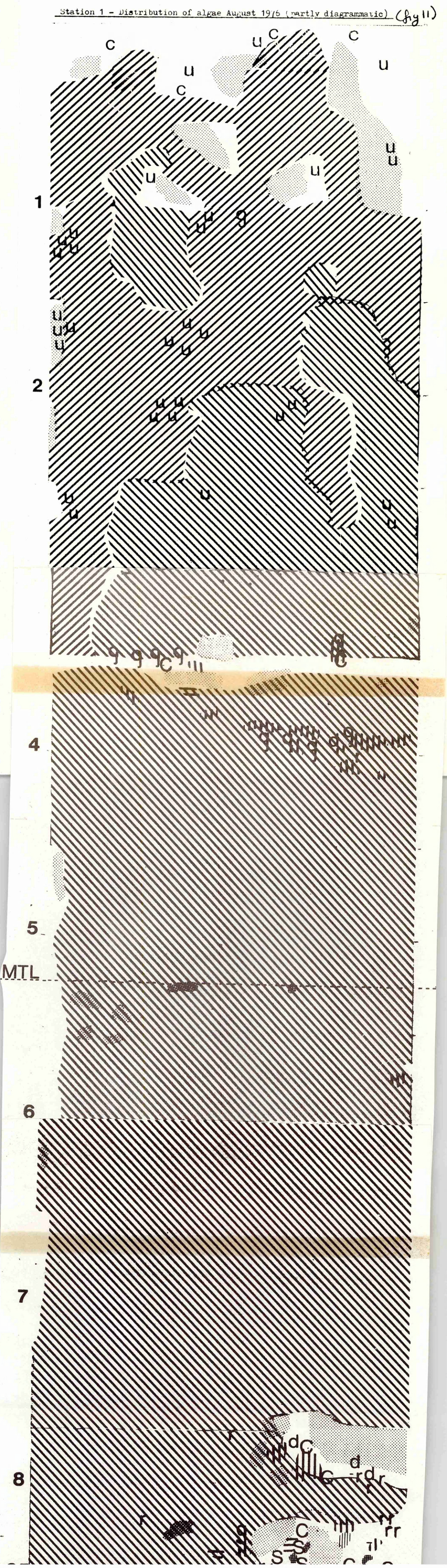


Figure 12 - Station 1 - Distribution of algae August 1977

(partly diagrammatic)

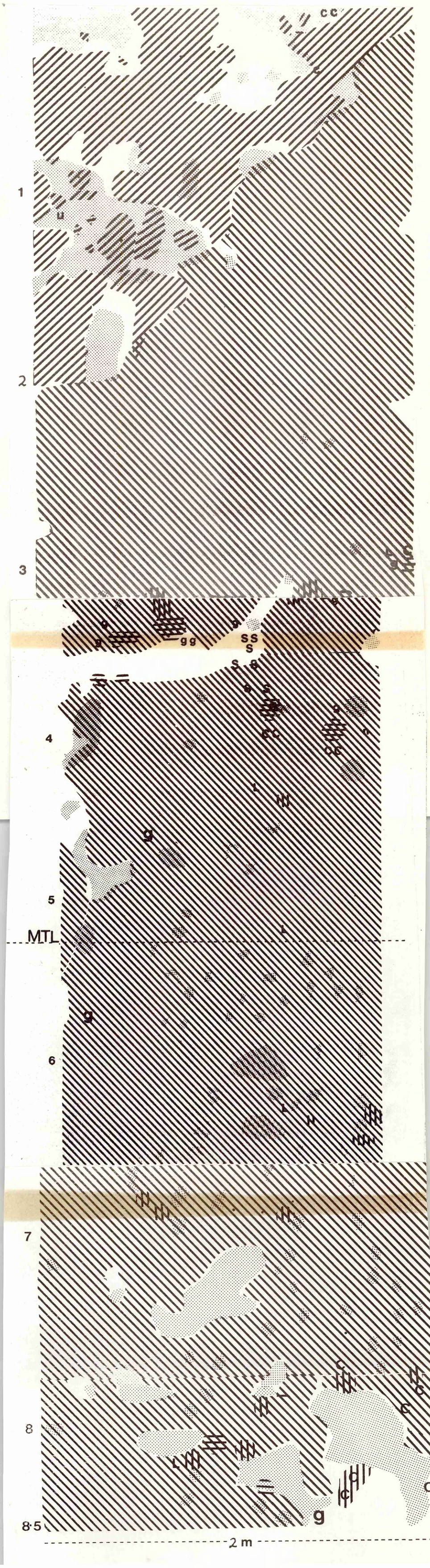


Figure 13 - Station 1 - Control area - February 1975

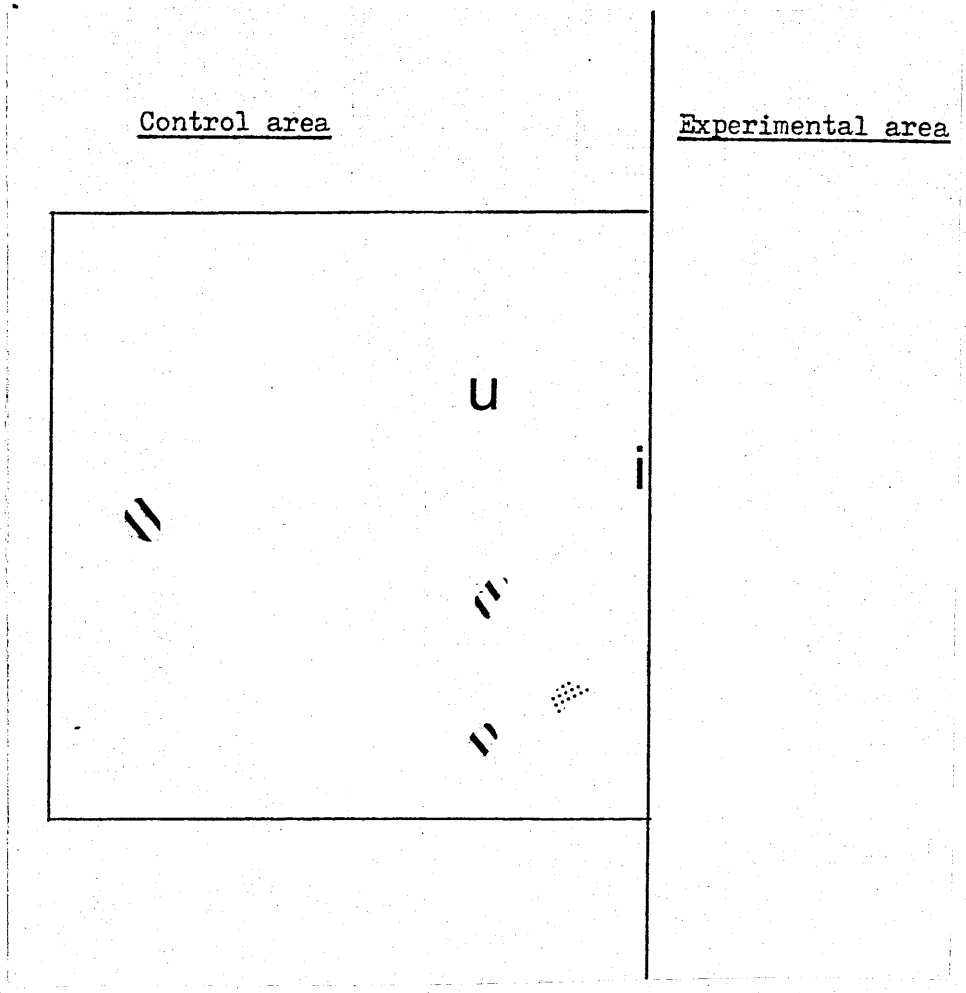


Figure 14 - Station 1 - Control area - December 1976

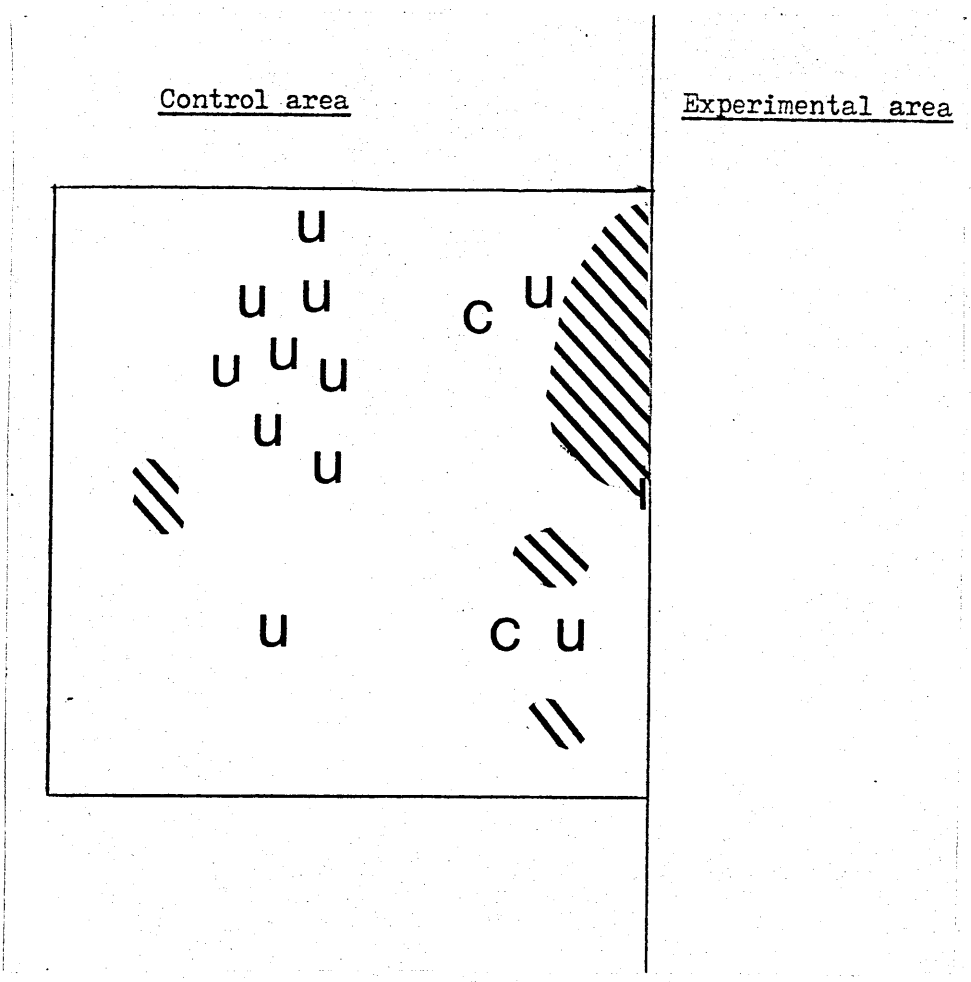


Figure 15 - Station 1 - Control area - August 1977

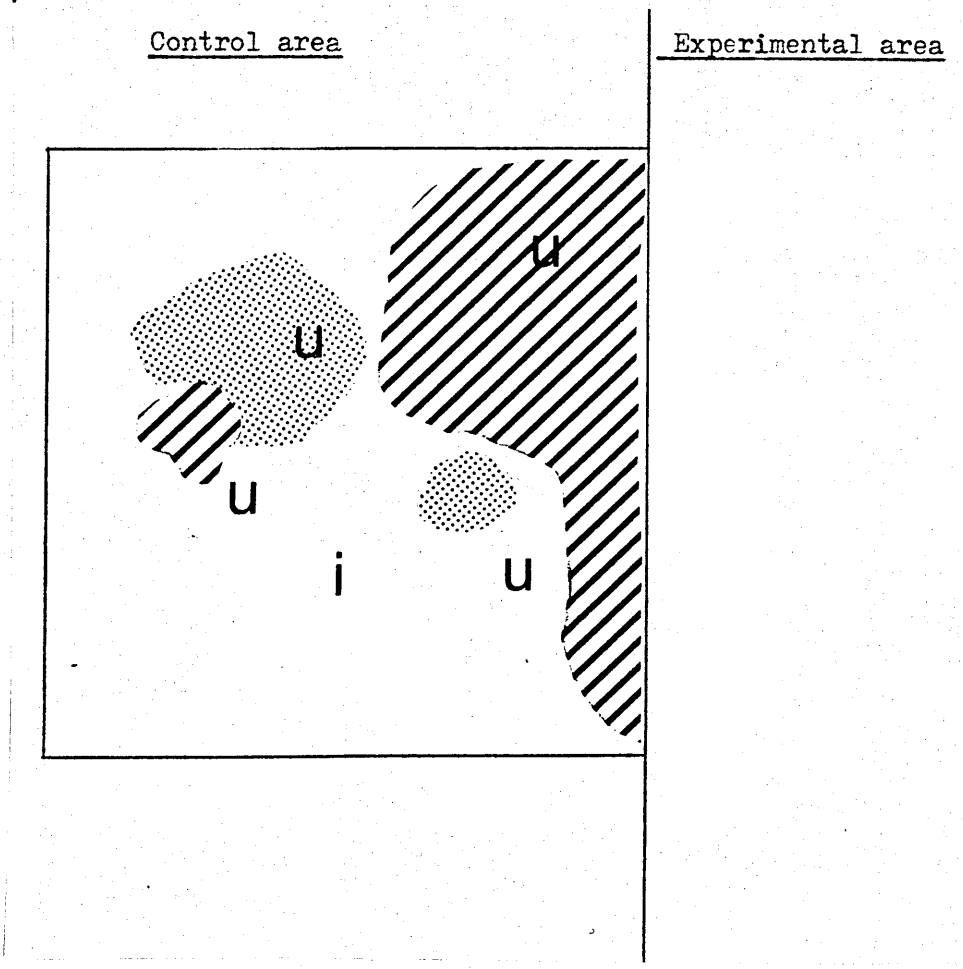


Figure 16 - Station 2 - Distribution of algae - August 1974

(partly diagrammatic)

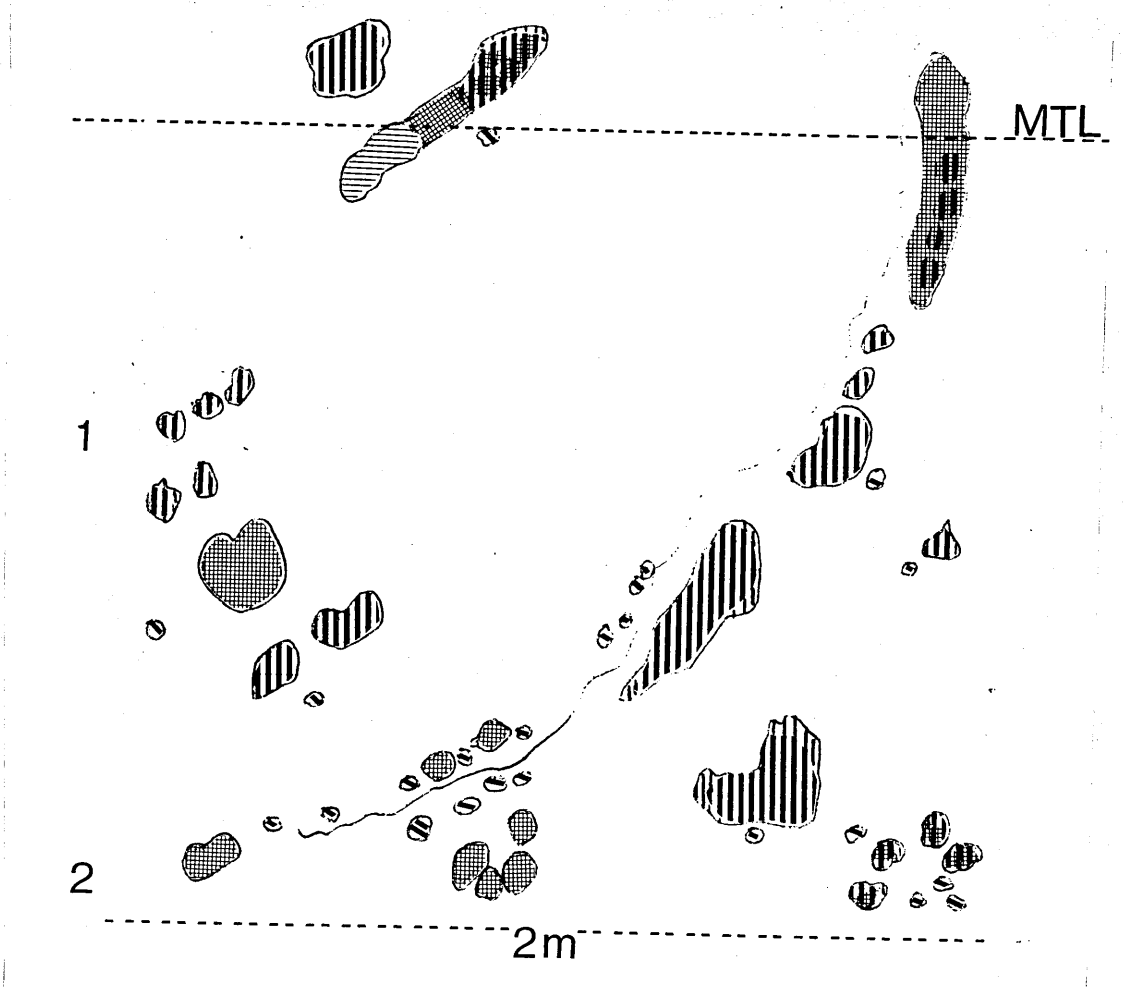


Figure 17 - Station 2 - Distribution of algae August 1975

(partly diagrammatic)

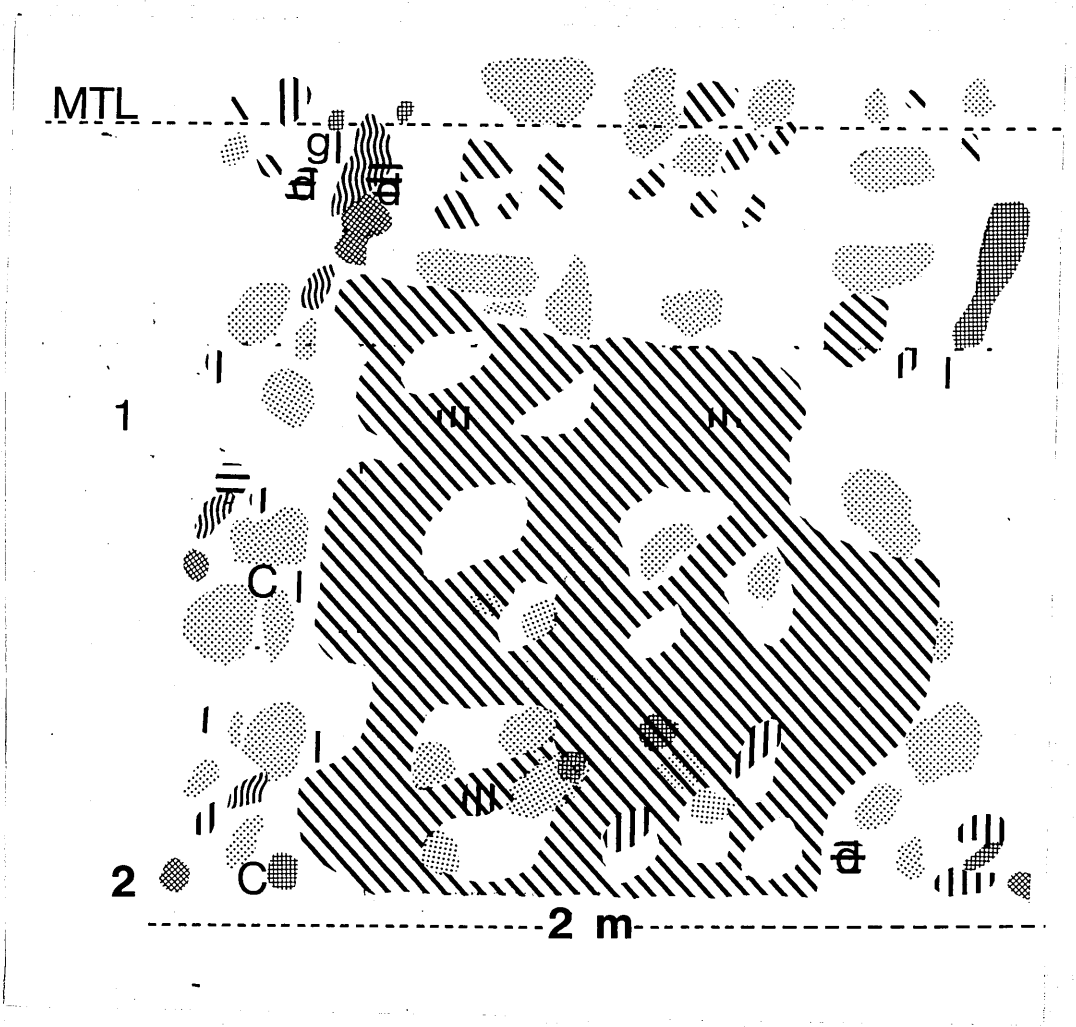


Figure 18 - Station 2 - Distribution of algae August 1976

(partly diagrammatic)

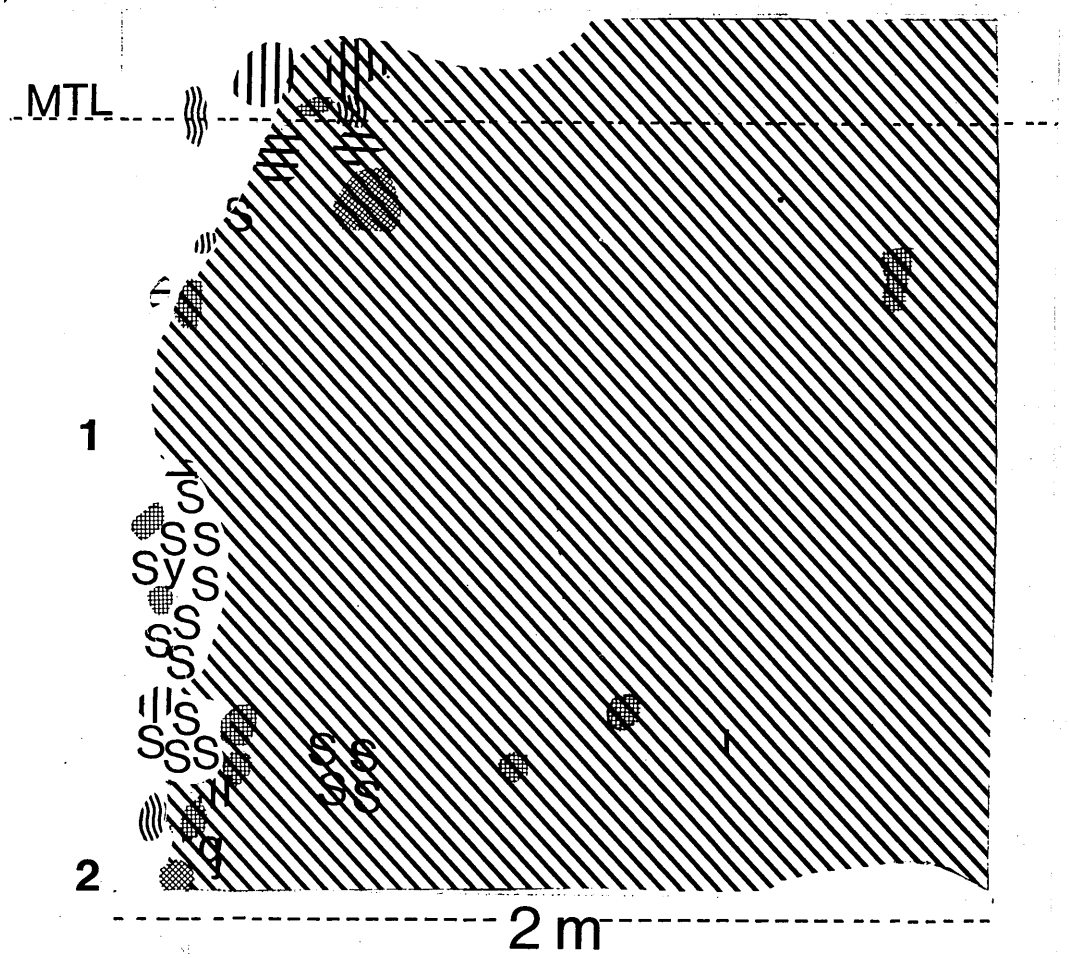


Figure 19 - Station 2 - Distribution of algae August 1977

(partly diagrammatic)

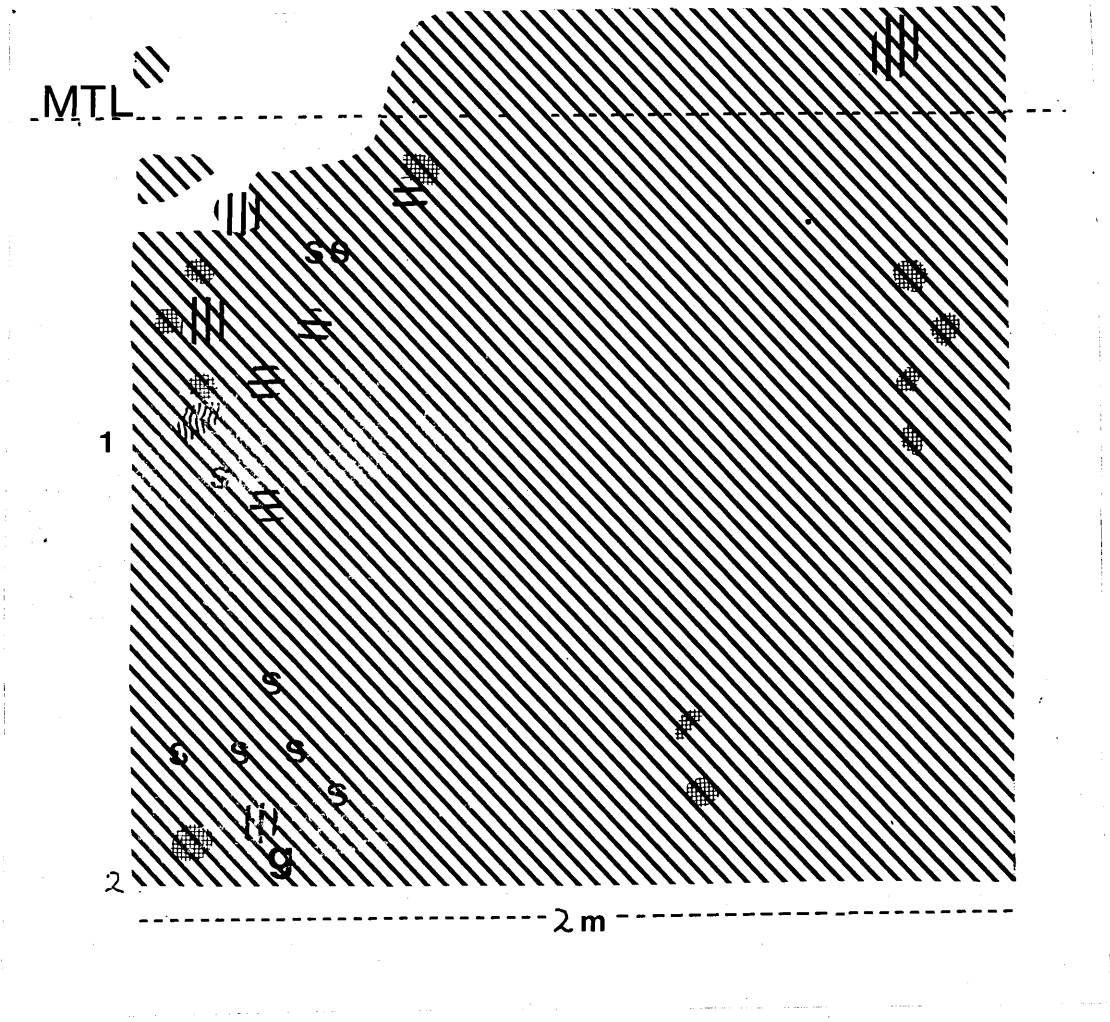


Figure 20 - Station 2 - Control area - February 1975

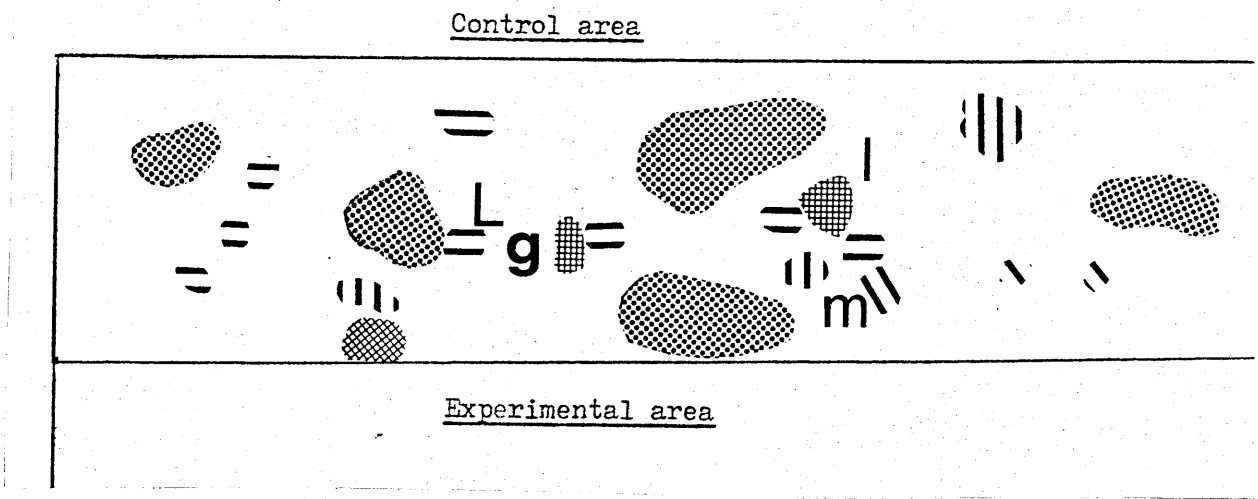


Figure 21 - Station 2 - Control area - July 1976

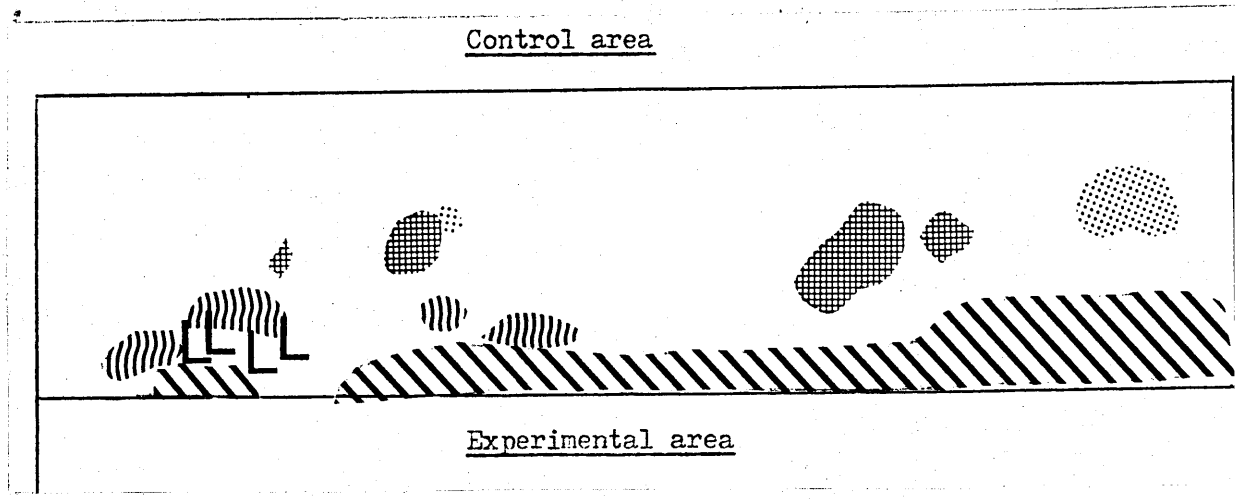


Figure 22 - Station 2 - Control area - August 1977

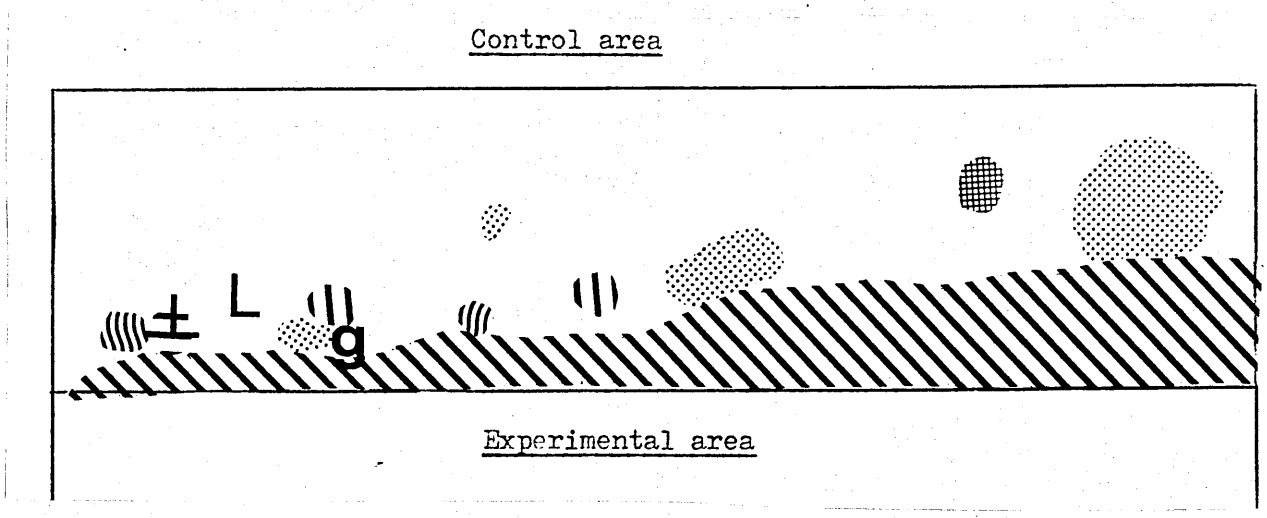
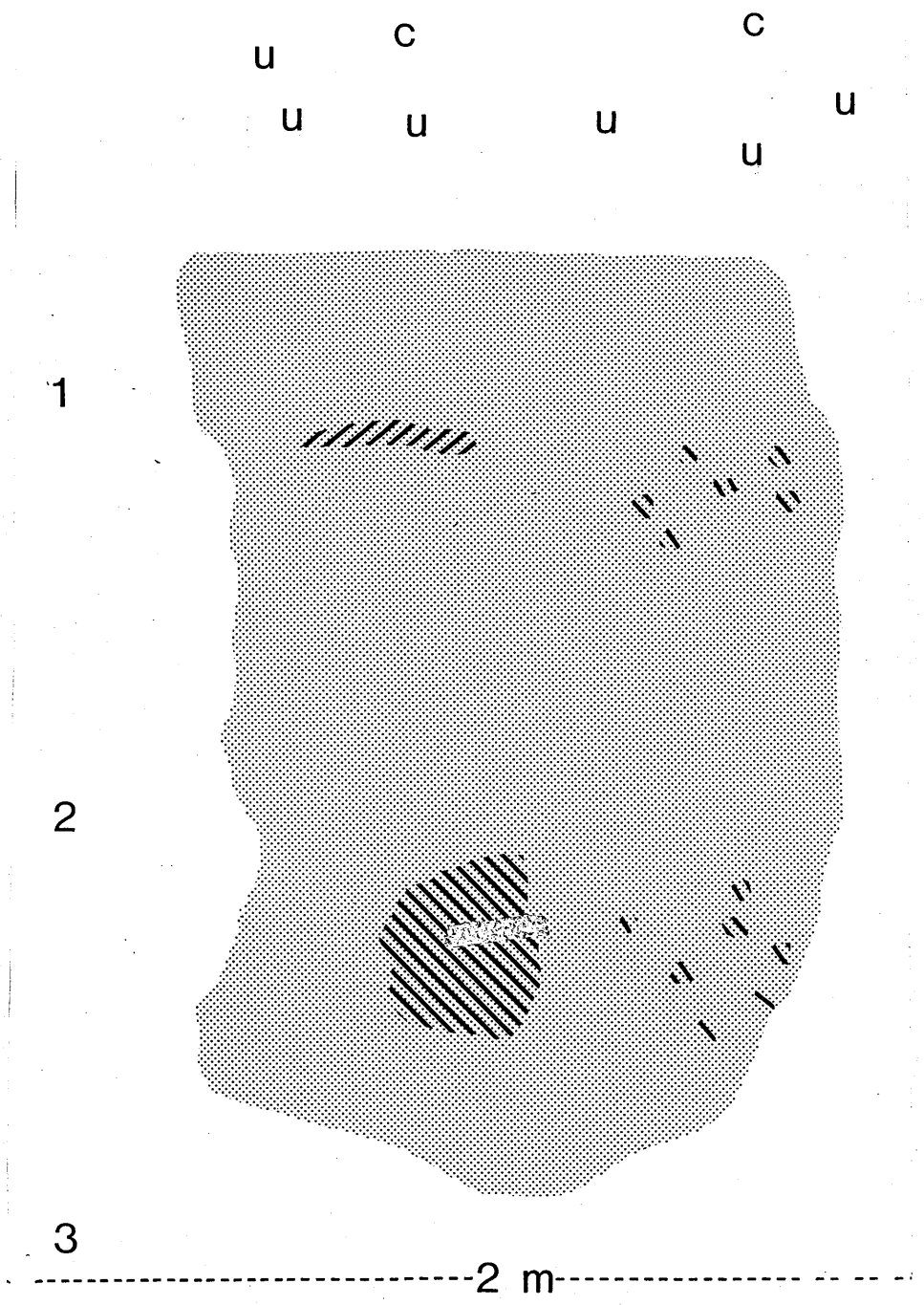


Figure 23 - Station 3 - Distribution of algae August 1975

(partly diagrammatic)



No algal growth observed during August 1974.

Figure 24 - Station 3 - Distribution of algae August 1976

(partly diagrammatic)

Figure 25 - Station 3 - Distribution of algae August 1977

(partly diagrammatic)

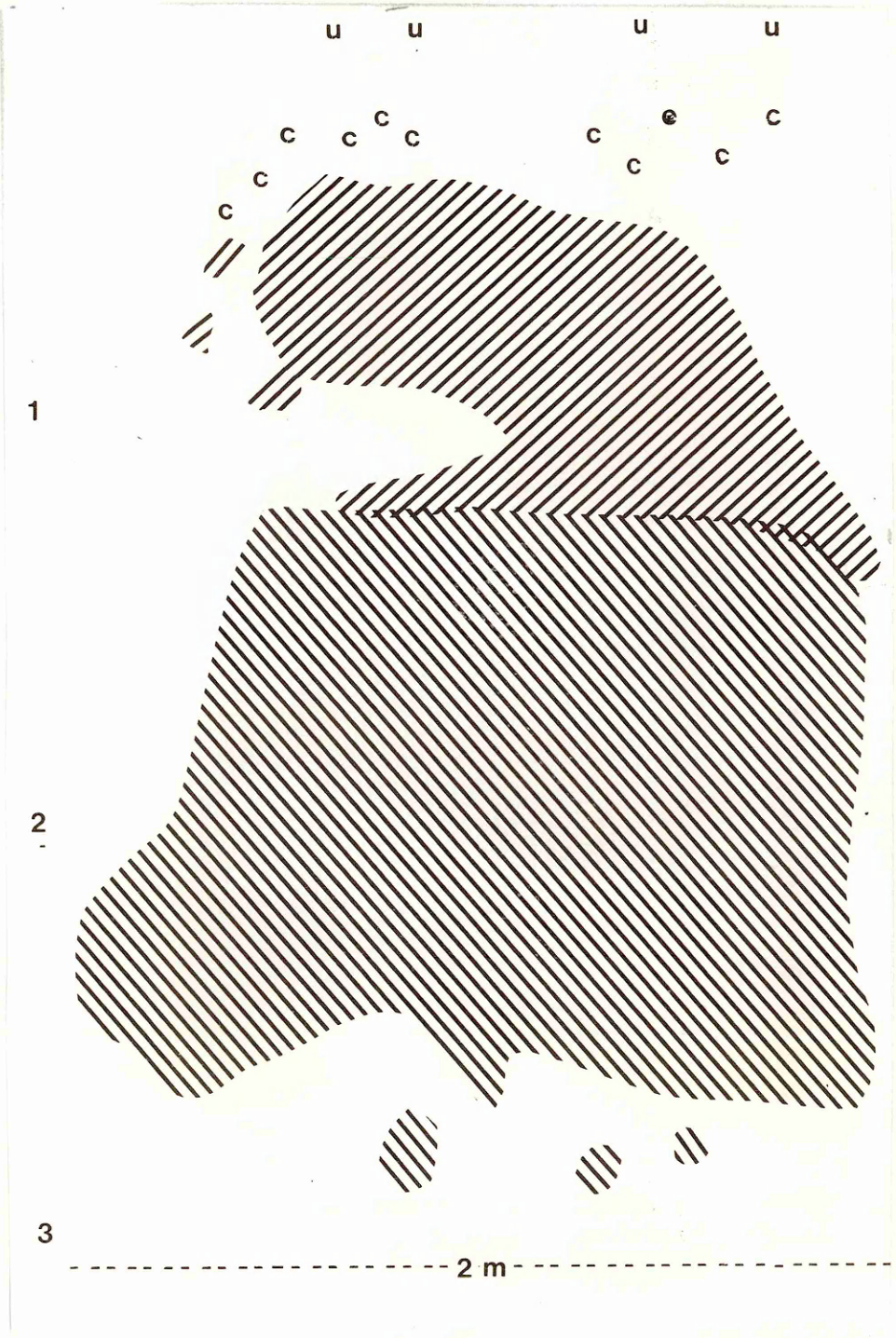
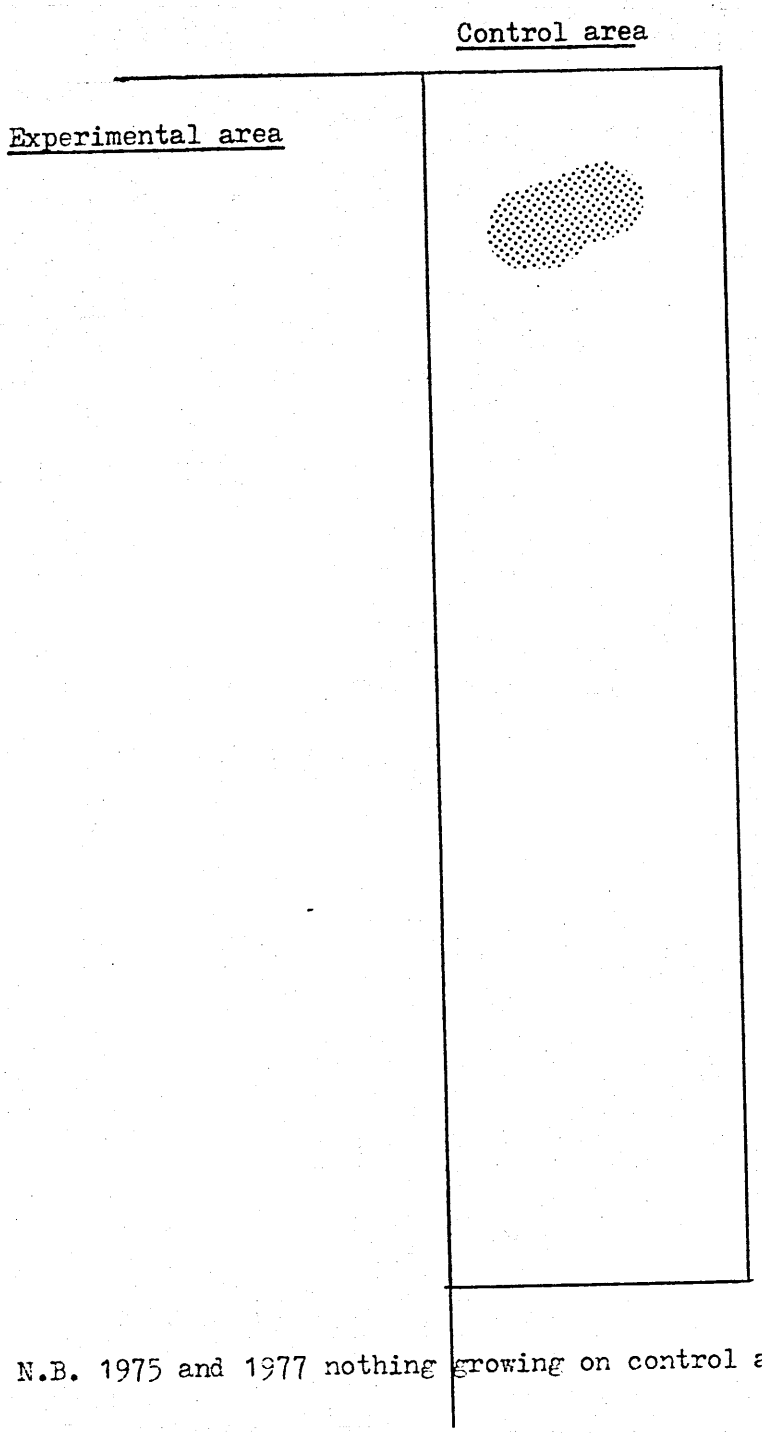


Figure 26 - Station 3 - Distribution of algae August 1976

(partly diagrammatic)



N.B. 1975 and 1977 nothing growing on control area.

Figure 27 - Station 4 - Distribution of algae August 1974

(partly diagrammatic)

Figure 28 - Station 4 - Distribution of algae August 1975

(partly diagrammatic)

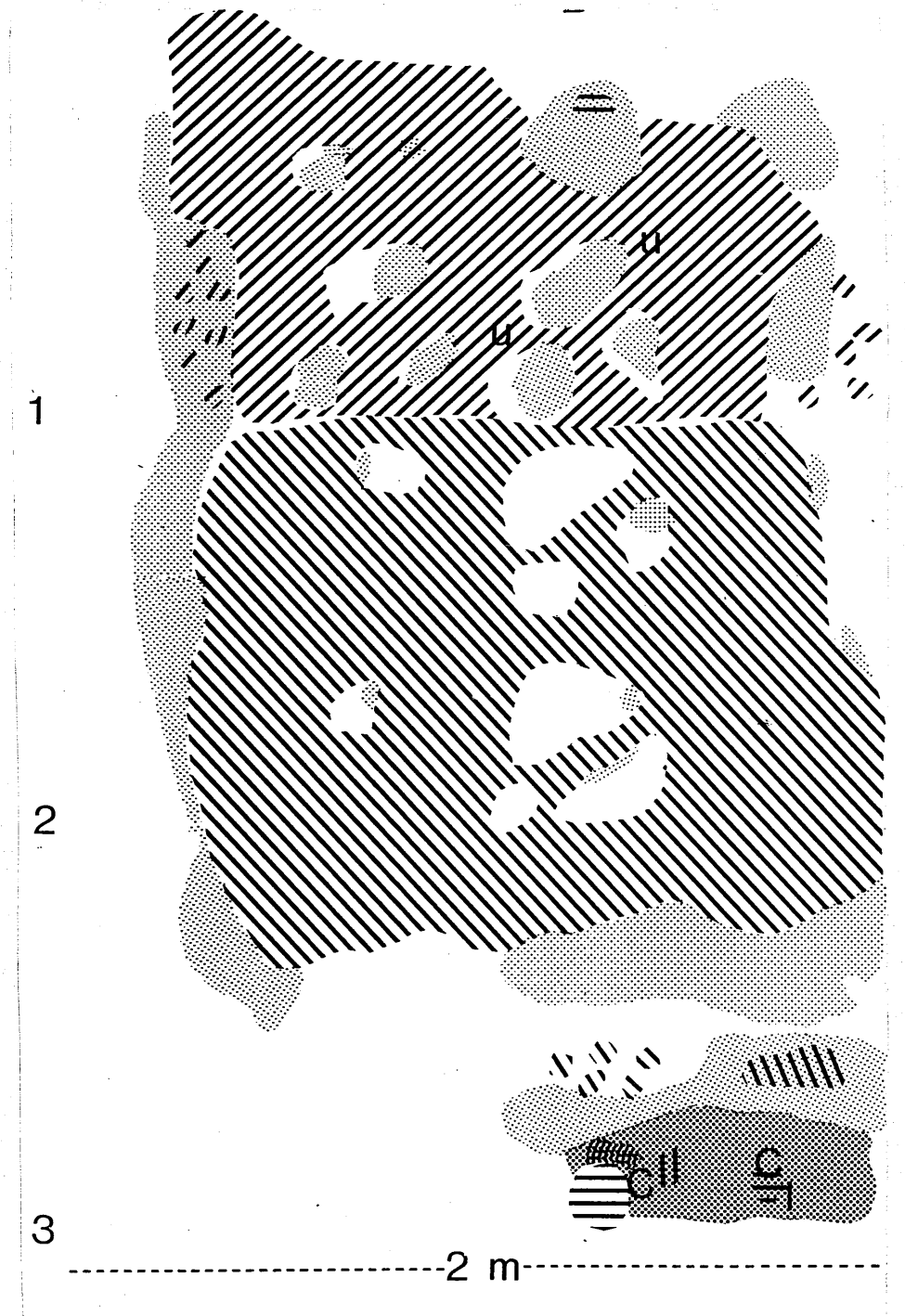


Figure 29 - Station 4 - Distribution of algae August 1976

(partly diagrammatic)

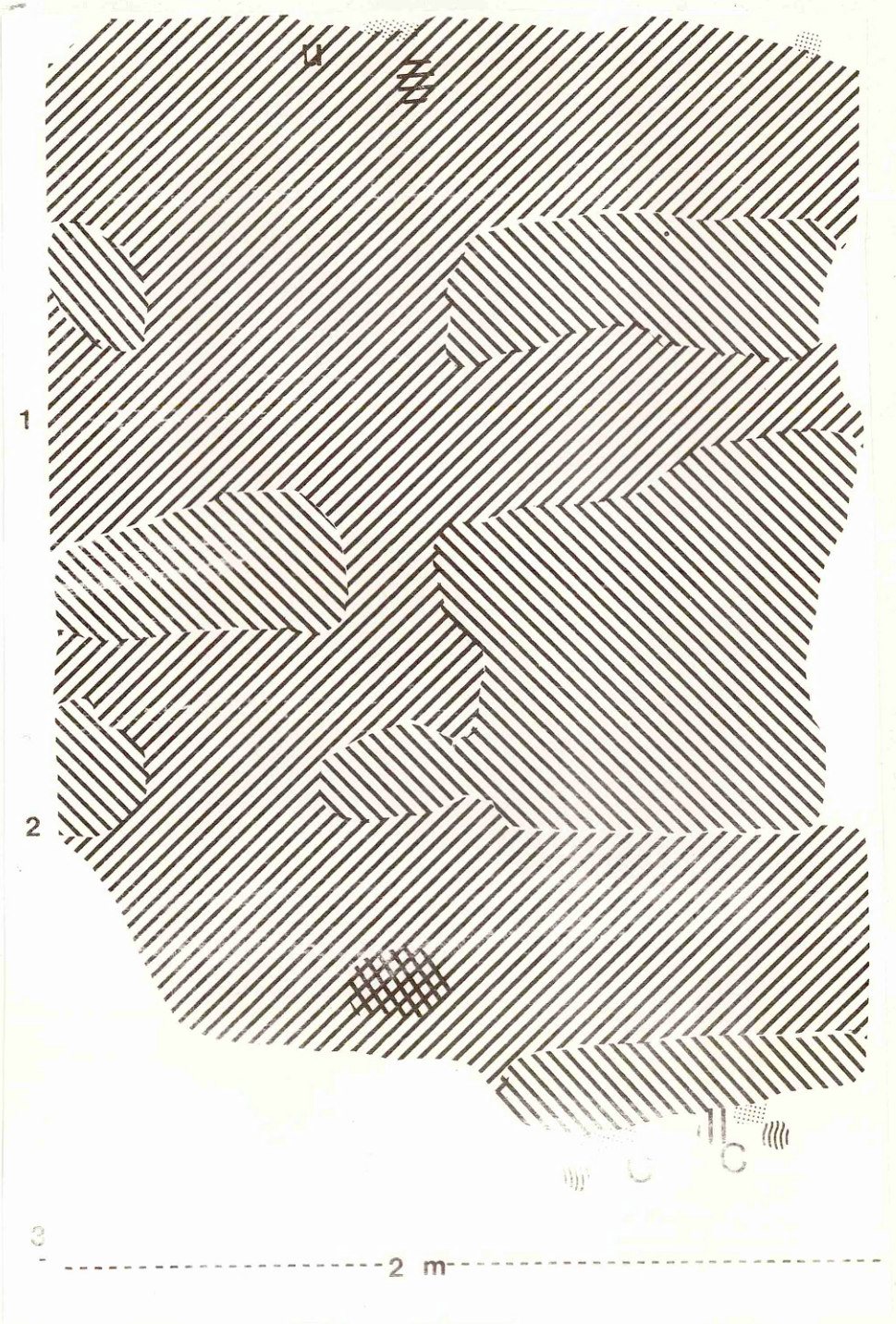


Figure 30 - Station 4 - Distribution of algae August 1977

(partly diagrammatic)

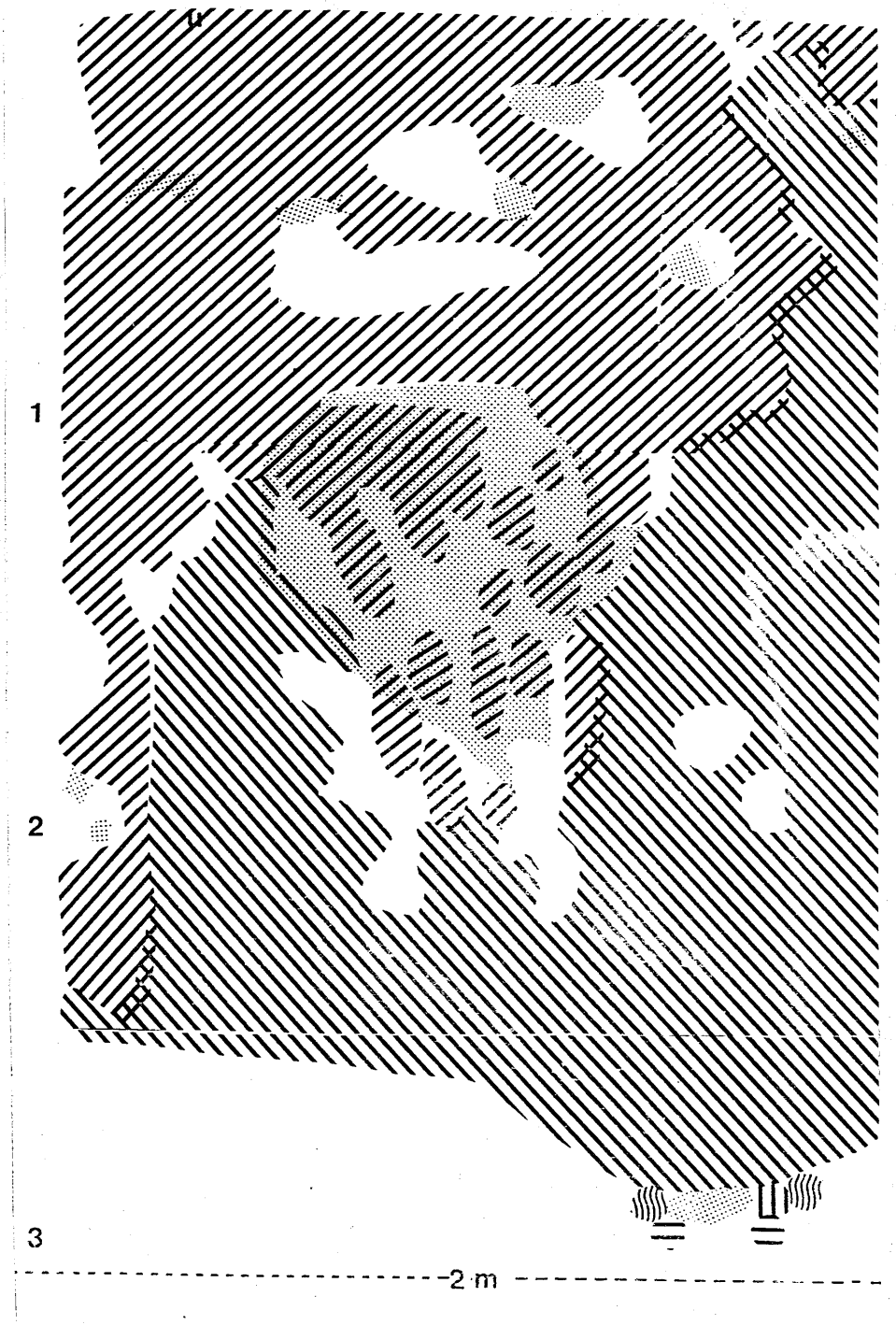


Figure 31 - Station 4 - Control area - June 1975

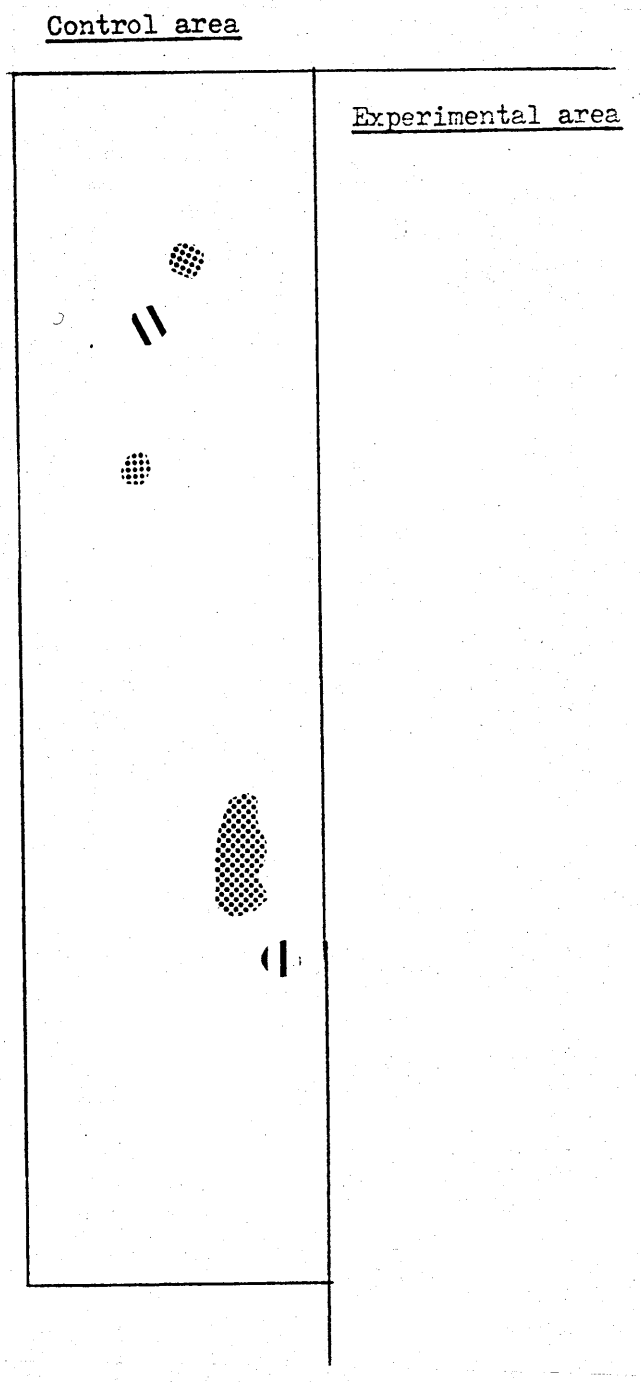


Figure 32 - Station 4 - Control area - July 1976

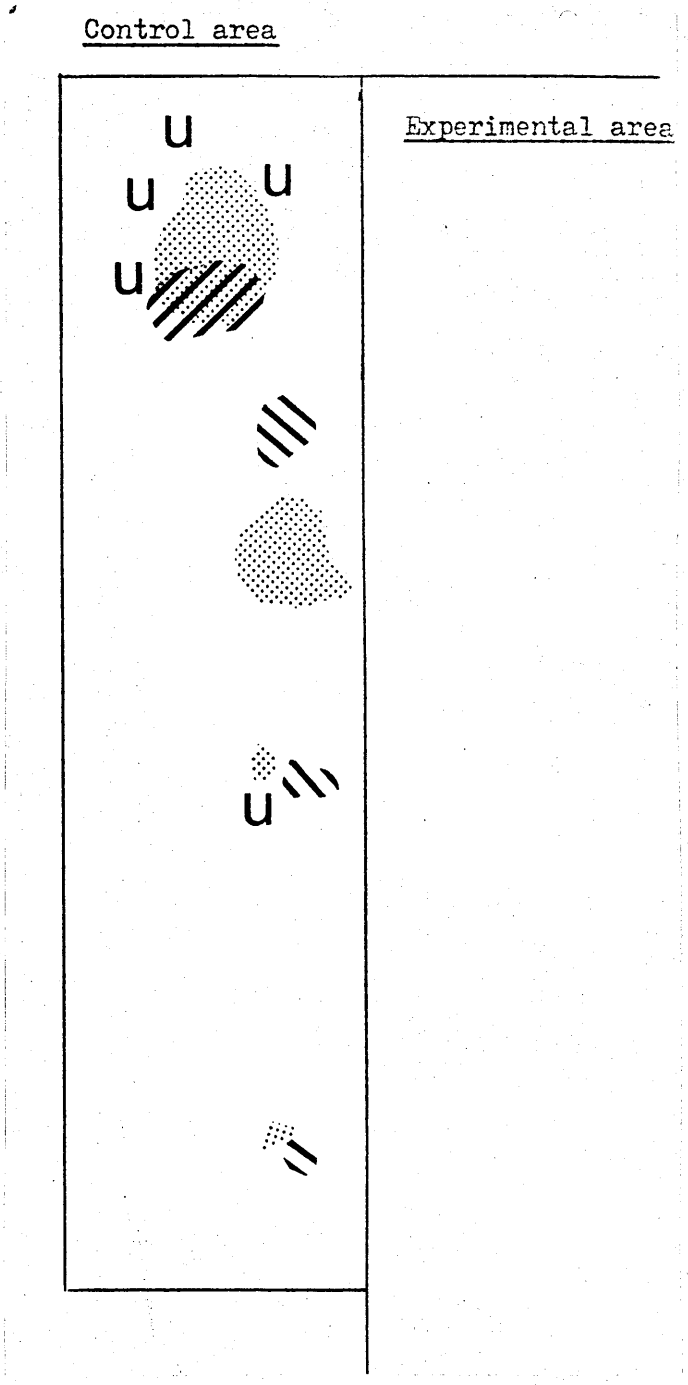


Figure 33 - Station 4 - Control area - August 1977

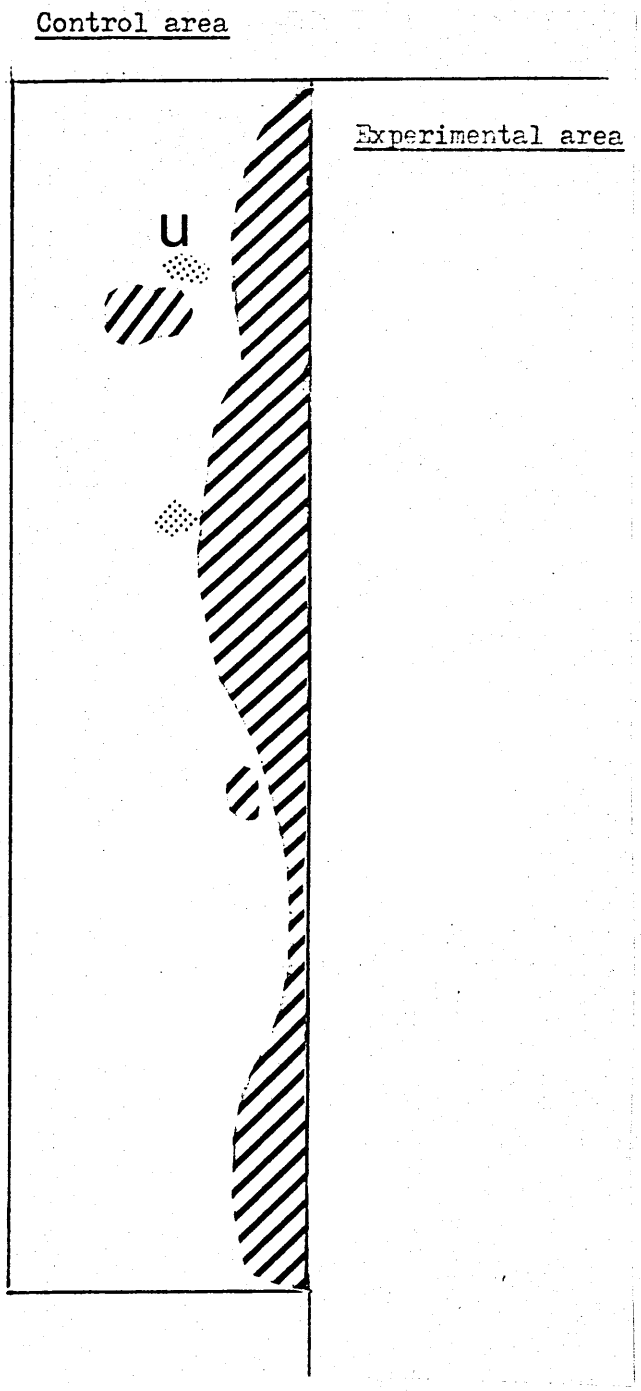


Figure 34 - Station 5 - Distribution of algae August 1974

(partly diagrammatic)

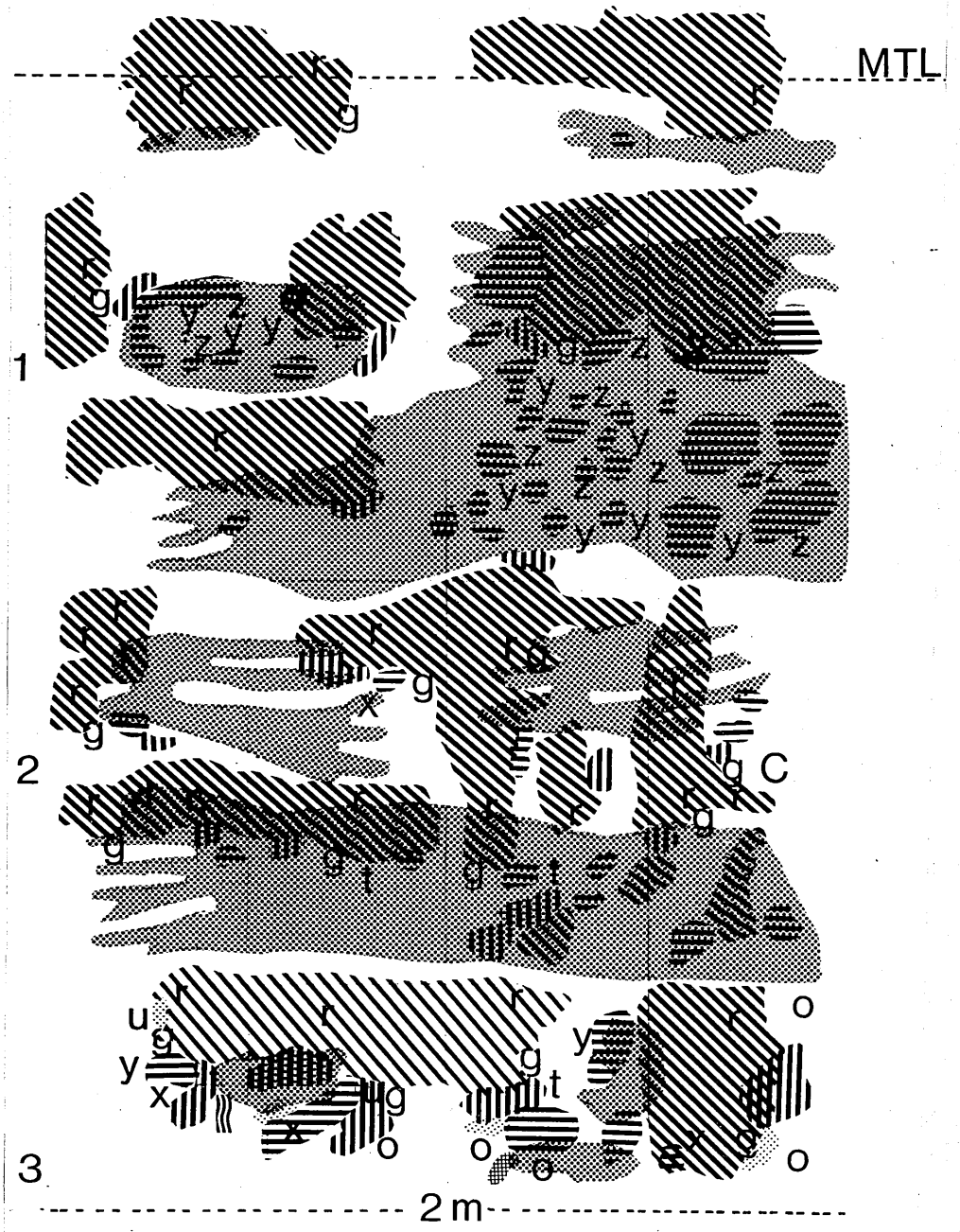


Figure 35 - Station 5 - Distribution of algae August 1975

(partly diagrammatic)

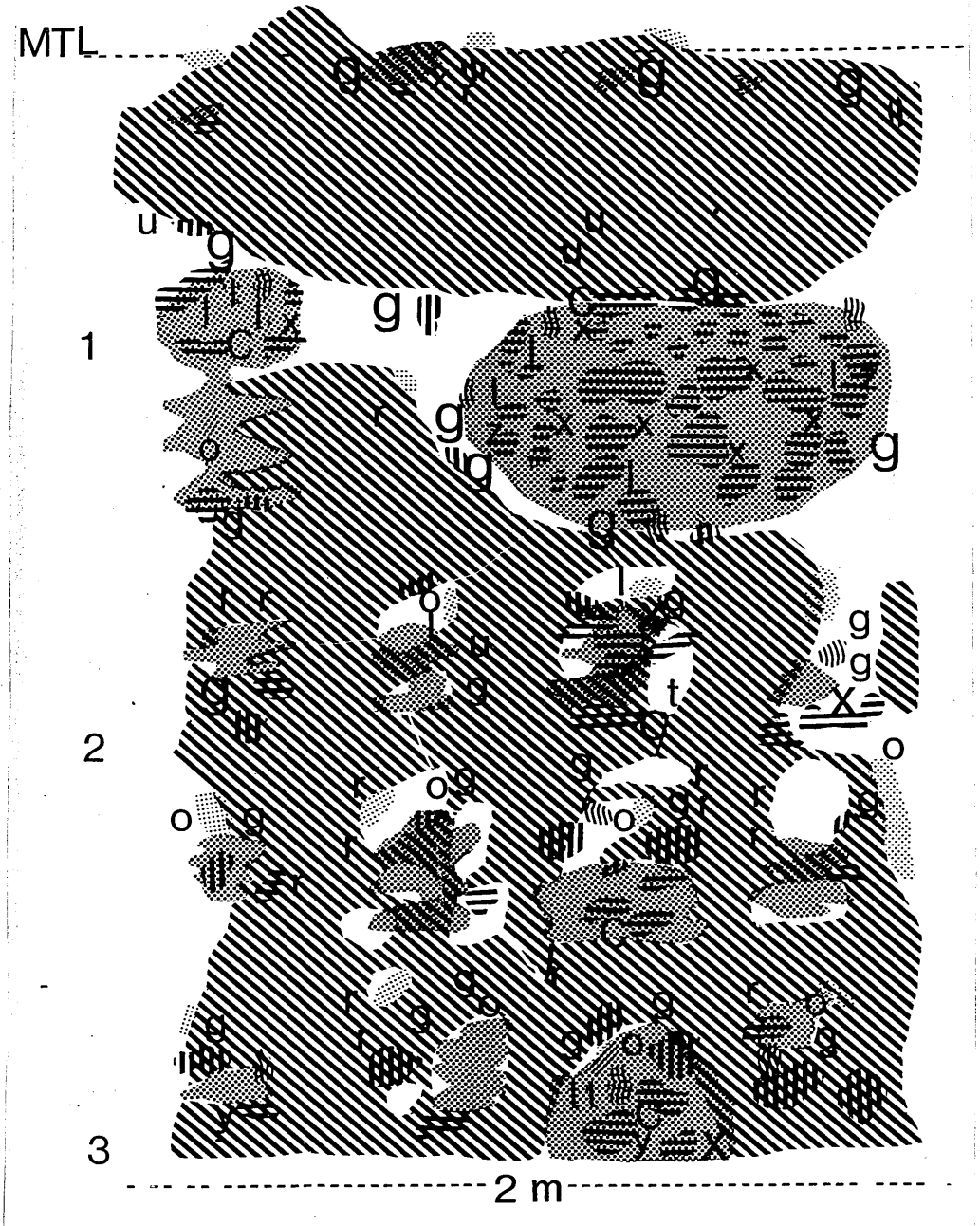


Figure 36 - Station 5 - Distribution of algae 1976

(partly diagrammatic)

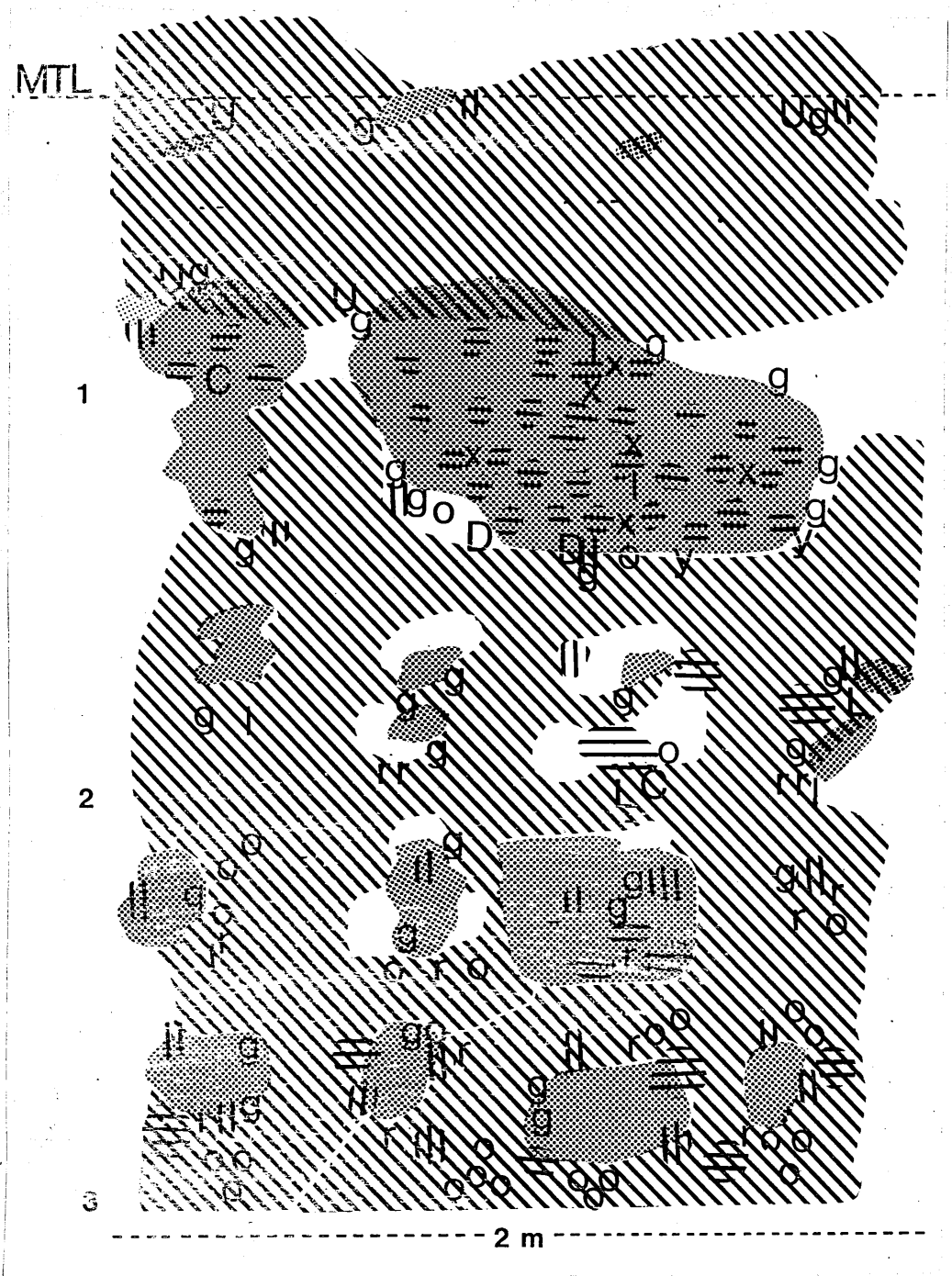


Figure 37 - Station 5 - Distribution of algae 1977

(partly diagrammatic)

Figure 38 - Station 5 - Control area - 1975

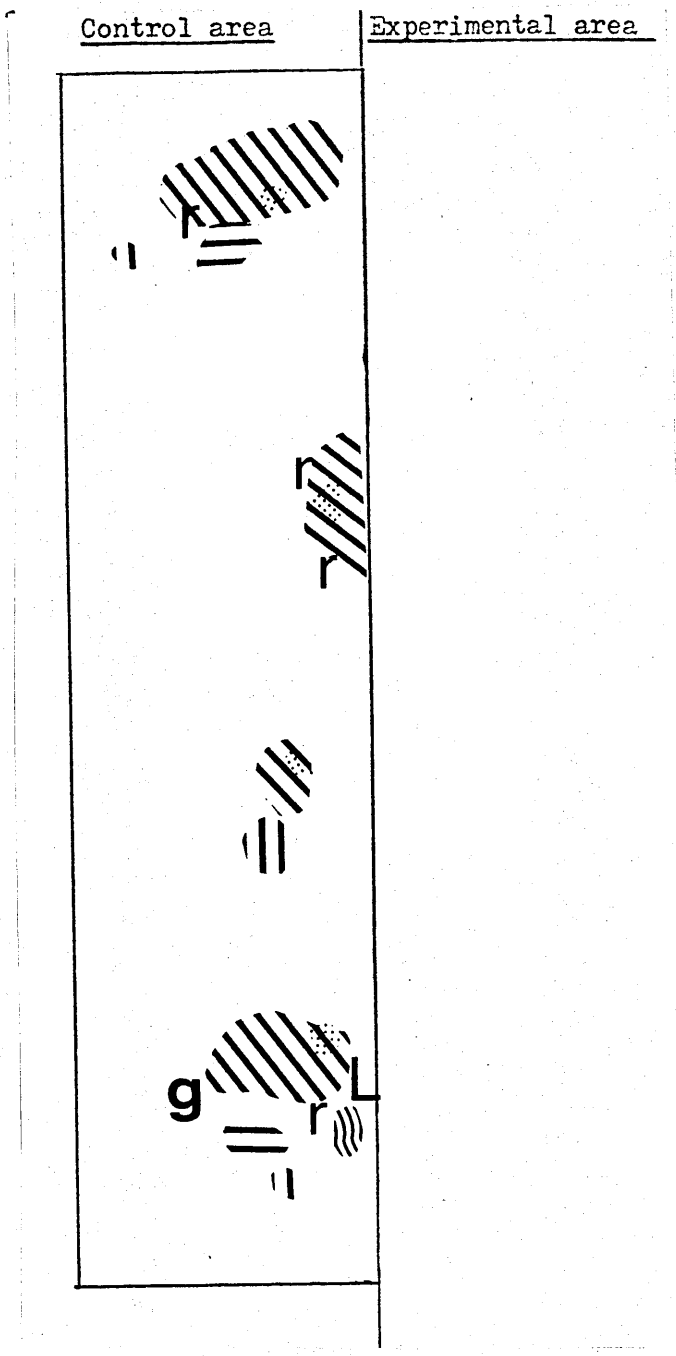


Figure 39 - Station 5 - Control area - July 1976

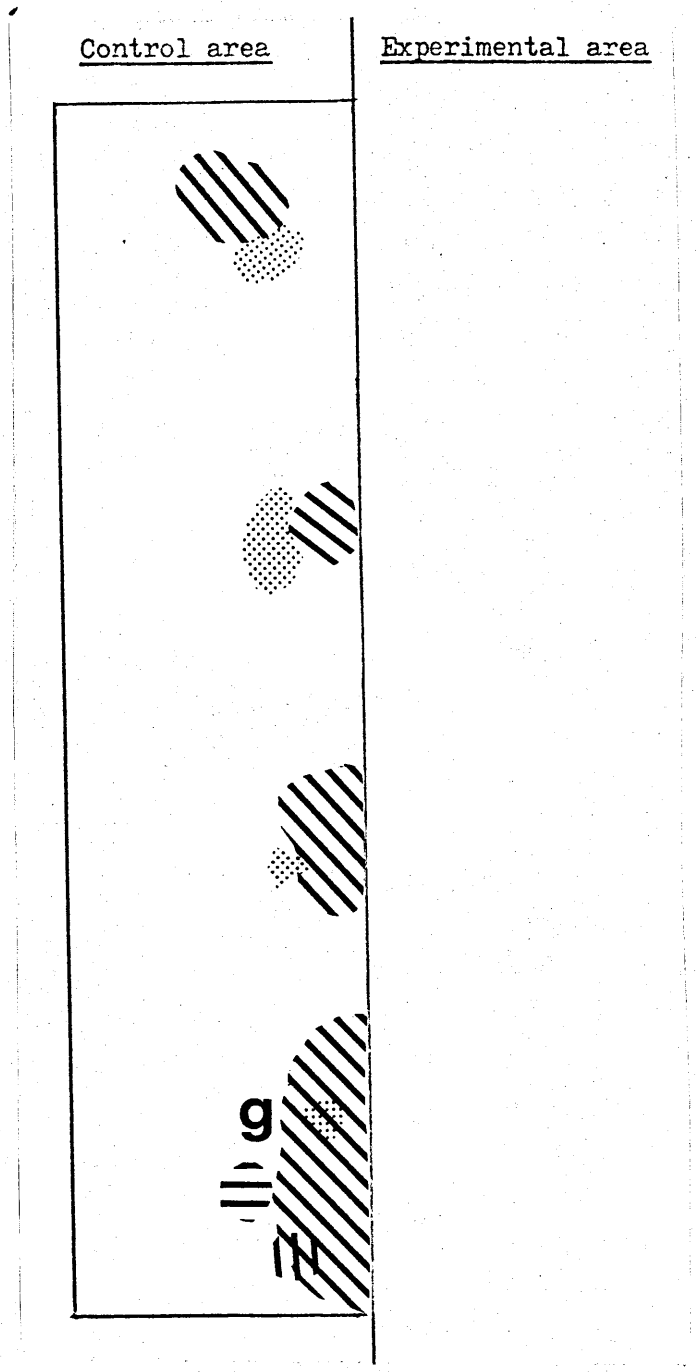
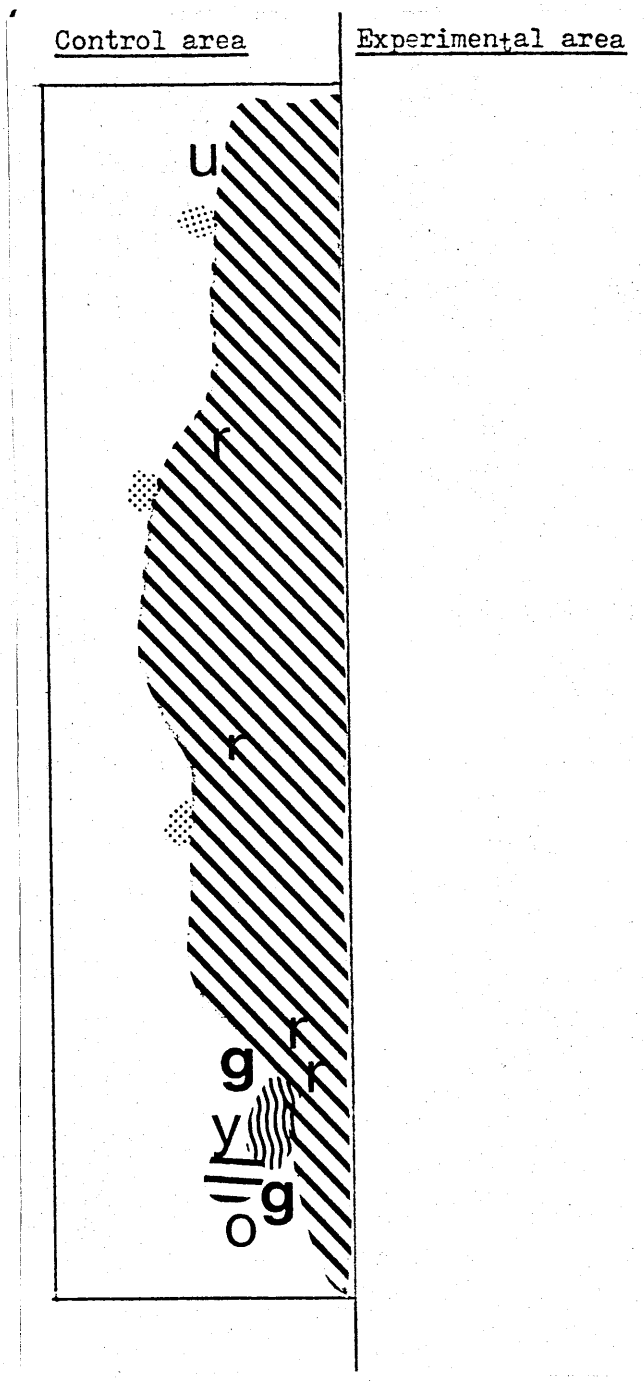


Figure 40 - Station 5 - Control area - August 1977



4.2 Algal species colonising experimental and control areas.

4.2.1 Algae growing on experimental areas August 1974.

Station	Phaeophycae	Rhodophycae	Chlorophycae
1	Pelvetia canaliculata Fucus spiralis F. vesiculosus F. serratus	Corallina officinalis Laurencia pinnatifida Ceramium shuttleworthium Lithothamnion spp. Lomentaria articulata Palmaria palmata	Enteromorpha spp. Cladophora rupestris Ulva lactuca
2	F. vesiculosus Leathesia difformis	Laurencia pinnatifida Corallina officinalis Gelidium corneum	Cladophora rupestris Enteromorpha spp.
3	-	-	-
4	F. spiralis F. vesiculosus Ectocarpus spp.	Corallina officinalis Lithothamnion spp. Porphyra umbilicalis	Entero morpha spp.
5	F. vesiculosus Himanthalia elongata	Palmaria palmata Lomentaria articulata Laurencia pinnatifida Corallina officinalis Gigartina stellata Ceramium shuttleworthium Polysiphonia nigrescens Callithamnium tetragonum Lithothamnion spp. P. umbilicalis Pterosiphonia thuyoides.	Enteromorpha spp. Chaetomorpha spp. C. rupestris

4.2.2 New species colonising the experimental areas August 1975.

Station	Phaeophycae	Rhodophycae	Chlorophycae
1	Leathesia difformis	Porphyra umbilicalis Gigartina stellata Ceramium flabelligerum	Enteromorpha linza Chaetomorpha spp.
2	Elachista fucicola	Gigartina stellata Ceramium flabelligerum C. shuttleworthium Polysiphonia nigrescens Lithothamnion spp. Chondrus crispus	Chaetomorpha spp. Enteromorpha linza Ulva, lactuca
3	Fucus vesiculosus	Porphyra umbilicalis	Enteromorpha spp.
4	Leathesia difformis	Laurencia pinnatifida Ceramium shuttleworthium Gigartina stellata	Enteromorpha linza Ulva lactuca Chaetomorpha spp.
5	Elachista fucicola Leathesia difformis	Ceramium flabelligerum C. rubrum Polysiphonia Brodiae P. urceolata Apoglossum ruscifolium	Ulva lactuca

4.2.3 New species colonising the experimental areas August 1976.

Station	Phaeophycae	Rhodophycae	Chlorophycae
1	-	Polysiphonia nigrescens	-
2	Fucus serratus	-	-
3	Pelvetia canaliculata F. spiralis	-	-
4	-	-	-
5	Laminaria digitata Alaria esculenta	-	-

4.2.4 Algae growing on control areas August 1974.

Identical to experimental area.

4.2.5 Species colonising the control areas in August 1975.

Station	Phaeophyceae	Rhodophyceae	Chlorophyceae
1	Fucus vesiculosus	Porphyra umbilicalis	Enteromorpha intestinalis
2	F. vesiculosus	Lithothamnion spp. Corallina officinalis Laurencia pinnatifida Lomentaria articulata Gigartina stellata Gelidium corneum Dumontia incrassata	Ulva lactuca Cladophora rupestris
3	-	-	-
4	F. vesiculosus	Lithothamnion spp. L. pinnatifida	
5	F. vesiculosus	C. officinalis L. pinnatifida Palmaria palmata L. articulata G. stellata	E. intestinalis Chaetomorpha spp.

4.2.6 New species colonising control areas in August 1976.

1	Pelvetia canaliculata		
2	-	-	Chaetomorpha spp E. intestinalis
3	-	-	E. intestinalis
4	F. spiralis	P. umbilicalis	E. intestinalis
5	-	-	-

4.2.7 New species colonising control areas in August 1977

Station	Phaeophyceae	Rhodophyceae	Chlorophyceae
1	-	-	-
2	-	-	-
3	-	-	-
4	-	-	-
5	Himanthalia elongata	Porphyra umbilicalis Polysiphonia spp.	

4.3 The number of algal species colonising the experimental and control areas from 1974 - 1977.

Species numbers increased in the experimental areas between 1974 and 1977. On Station 1 the number of species increased by almost 50% from 13 - 20 over a period of three years. Species numbers more than doubled on Station 2 from 7 - 18 species. Five species colonised Station 3 between 1974 and 1977, whereas there was no algal growth before 1974. Species numbers doubled on Station 4 and increased by 62% on Station 5 (see Table 6).

Species numbers hardly varied on the control areas. Only one new species each on Stations 1 and 3, two on Station 2 and three on Stations 4 and 5 (see Table 6).

TABLE 6 - The number of species colonising experimental and control areas between 1974 and 1977.

Experimental areas (1974 - 1977)

Station	Size of area	Number of Species Aug 1974 (initial species)	Aug 1975 (new species)	Aug 1976 (new species)	Aug 1977 (new species)	Total Number of Species 1974 - 1977	Increase in Species numbers
1	$33m^2$	13	6	1	0	20	7
2	$4m^2$	7	10	1	0	18	11
3	$6m^2$	0	3	2	0	5	5
4	$6-6.5m^2$	7	7	0	0	14	7
5	$6m^2$	16	8	2	0	26	10

Control areas (1975 - 1977).

		Number of Species 1975	1976	1977		
1	$1m^2$	3	1	0	4	1
2	$1m^2$	10	2	0	12	2
3	$1m^2$	0	1	0	1	1
4	$1m^2$	3	3	0	6	3
5	$1m^2$	8	0	3	11	3

Number of species based on results Section 4.2.

5. DISCUSSION

5.1 Re-colonisation on exposed shores

The most striking feature found on all the experimental areas was the rapid algal colonisation of almost bare rock after limpet clearance. This was observed on all the experimental areas but was less obvious on Station 3. In August 1974 most of the rock surfaces were sparsely covered with algae but within weeks of limpet clearance a film of microscopic filamentous and blue green algae covered the experimental areas of each station. This covering did not occur on the control areas which continued to be grazed by limpets.

Jones (1948) had observed that limpets will graze an apparently bare rock surface. He concluded that there must be some form of microscopic alga growing on the rock surface. This was confirmed by the above observations. Jones also observed a link between the number of limpets present on a given area of rock and the quantity of alga present. In the present study very large numbers of limpets were removed from each experimental area (in excess of 100 adults per square metre), which showed only sparse algal growth.

The algal film eventually disappeared and was replaced by various algae including Enteromorpha intestinalis. These were in turn succeeded by fucoids such as F. spiralis and F. vesiculosus var. evesiculosus (henceforth to be known as F. vesiculosus since the

vesicular form did not occur in this locality). This pattern of algal succession was found on all experimental areas but did not always occur at exactly the same rate., e.g., it took two years for F. spiralis to become established on Station 3, whereas the same species formed dense "mats" on other stations within one year.

The presence of adjacent control areas allowed comparisons to be made with the experimental areas at each station. It was observed that algal colonisation and growth was much slower in these control areas. Limpets continued to graze the control areas, therefore, it must be concluded that their feeding activities affected algal colonisation and growth. It is, therefore, reasonable to assume that it was limpet clearance that brought about increased colonisation and growth in the experimental areas.

These observations confirm the work of Moore (1938), Conway (1946), Jones (1946) and Lodge (1948) on limpet grazing and its effect on algal colonisation. The phenomenon of algal succession on cleared areas as observed by Pyefinch (1943), Jones and Lodge is also broadly confirmed by the present study.

Certain differences were, however, observed, notably in the rate of colonisation and it will be argued that this results primarily from the greater exposure of the sites studied. The rate of change varies from site

to site even when situated near each other e.g., Station 3 showed slower re-colonisation than Station 1 of the present study. This can be explained in terms of local differences on the rock surface such as different rates of exposure or slope of rock.

Several workers have described the replacement of green algae by brown on cleared areas (e.g., Jones (1946), Southward (1964). Some belived that the greens prepared the rock surface in some way for the establishment of fucoid sporelings. Others have stated that green algae have a faster growth rate than the brown which results in them colonising a rock surface more rapidly. The brown algae eventually catch up with the greens and overtake them. The resulting rapid growth of the browns blocks out light from the underlying greens and they disappear. The dominance of the fucoids over other algae was very obvious on all experimental areas in the present study.

The generally observed, early colonisation by green algae followed by brown may be a result of faster growth but it might also be a result of greater spore availability in the greens. Enteromorpha spp. for example, produce spores all the year round, the bulk appearing on the spring tides. These spores have the capacity to survive for some time in a viable state (probably for more than a week) and are able to attach very rapidly and grow quickly afterwards. Fucoids have

a more limited fruiting season and produce fewer eggs which are slower to attach. Green algae would, therefore, re-colonise a bare rock surface and become well established before the browns were able to do so, this would give the appearance of succession.

Some of the results of the present study e.g., at Station 3, support the theory that the rapid colonisation of the bare rock surface by green algae is followed shortly afterwards by colonisation by fucoids (see Table 3). It was difficult to establish whether this was a true succession or the shading effect of canopy species smothering the underlying green algae such as E. intestinalis.

There is some controversy as to whether or not "weathering" of the bare rock is necessary before algal re-colonisation can take place. Connell (1972) believed that green algae only preceded brown algae because of the faster settlement of green spores. He maintained that the fucoids would colonise a rock surface anyway, without being preceded by greens. The results of the present study supported Connells' view (see, for example Tables 1, 4 and 5). At Stations 1, 4 and 5 the percentage cover of the fucoids increased with that of E. intestinalis. This implies that it is not necessary for the greens to "prepare" the rock surface in any way before the browns are able to colonise. Dayton (1975) and Southward (1978) however maintained that some degree of weathering was necessary before algal colonisation and succession could occur.

It is believed that within hours of clearing a rock surface of all visible living organisms it becomes covered by a layer of bacteria. Most bacteria contain mucilaginous or gelatinous material in their cell walls which enable them to adhere to each other or to any solid surface. Any algal spores which happen to touch the bacterial layer might adhere more easily and become established more quickly. This would be an advantage to delicate spores which must establish quickly in order to survive.

Spore attachment occurs purely by chance but it is likely that they attach more easily to a bare rock surface than to a surface covered with algae. It is believed that most adult algae produce chemicals that discourage spore attachment to their fronds. There are only a few epphytic algae e.g., Palmaria palmata that seem able to overcome this barrier. It may, therefore, be beneficial for the spores if clearance procedures are carried out as in the present study.

The question of algal succession i.e., green algae replaced by browns is complex and involves many factors. As stated previously green algae usually have faster spore settlement times than the brown algae. There is also the matter of spore availability, since many brown algae produce spores for only a few weeks during the year. This partly explains the fairly rapid colonisation of a cleared rock surface by green algae. This occurred on Station 1 of the present study (see Table 1) but if a different

location had been selected and a different time of year chosen for limpet clearance (spring and summer in the present study) the results may well have been different. The reason for this is that different algal spores would have been available for attachment resulting in a different attachment and succession pattern.

Lodge observed algal colonisation and succession on the limestone "steps" at Port Erin, Isle of Man. She also observed that limpets will migrate into the newly colonised areas and clear them eventually of algae. These observations were confirmed by the present study since limpets were continually moving into the five experimental areas. This was also observed by Aitken (1962) and Dayton (1971) since both workers had to remove limpets continually from their experimental areas if they were to have any re-colonisation at all.

In the present study the invading limpets were easy to locate and remove since they were always surrounded by a bare grazed patch of rock. It was impossible to visit the experimental areas as often as one would wish; this inevitably resulted in a migration back of limpets. Limpet spat were also brought in with the tide and settled on the experimental areas to create an even greater grazing effect. It is probably true to say that grazing occurred on a reduced level in the experimental areas compared with the controls.

Lewis and Bowman (1975) observed that young fucoid plants provided a very suitable habitat for limpet spat providing correct moisture levels and plenty of suitable food. As the algae increased in size spat settlement became more difficult, but adult limpets continued to migrate into the experimental areas. It is generally believed that most algae are grazed by limpets.

Pyefinch (1943) based his observations on individual rocks cleared of all fauna and flora. Lodge as mentioned previously used one long strip of rock which was presumably subjected to similar conditions of exposure, shading etc, along the whole of its length. Neither Lodge nor Pyefinch used control areas. This suggests that neither worker could prove conclusively that the events which they were describing were not occurring outside their experimental areas, although Lodge used the extensive algal growth on the experimental strip as a comparison with adjacent grazed areas.

Lodge also states that her investigations were carried out on a "moderately" exposed shore. The presence of Ascophyllum nodosum and the absence of F. vesiculosus var. evesiculosus however suggests that the area was in fact farily sheltered. The five experimental areas in the present study were definitely exposed areas of shore or very exposed areas of shore. Exposure did not seem to affect algal colonisation or algal succession but it does seem to influence the rate of colonisation. The control

area of Station 3 for example produced only one small area of alga in three years. Other control areas however produced fairly extensive if sparse growth. Colonisation of the experimental area of Station 3 was also slower than in other experimental areas as described previously. Heavy wave action damaged mature plants on other experimental areas leaving only the holdfasts. This was especially noticeable on Station 5.

Re-colonisation was not so badly affected by severe wave action on Station 5 as on Station 3. Station 5 was however more level than Station 3 (see figures 7 and 8) and also lower down the shore (see figure 5). It is therefore likely that position on the shore influences re-colonisation as well as other factors such as slope.

Different angles of slope could affect colonisation and growth rate. Station 3 had the steepest slope being an almost vertical rock surface. Wave action and subsequent run-off could be severe at this location and seemed to affect sporeling establishment. There was less growth at this Station than on any of the others. The effect of heavy wave action and run-off was also observed by Pyefinch on one of his experimental areas (the experimental area was in an exposed position).

Aspect did not seem to affect colonisation or growth unless there was heavy shading. Stations 1, 4 and 5 were south facing, Station 3 north facing and Station 2

was almost horizontal. Station 3 was shaded for part of the day and the upper zone of Station 1 was also shaded for part of the day. Station 3 did produce less algal growth than other Stations but it is difficult to say whether this was due to lack of light, heavy wave action or a steeply sloping surface.

The results of the present study indicated that abiotic factors such as exposure and wave action could affect algal colonisation. The steep slope and subsequent run-off observed at Station 3 resulted in slower and less extensive algal colonisation than on the other four experimental areas. Zonation was not affected however and zones of P. canaliculata. F. spiralis and F. vesiculosus developed normally. Fewer algal species were able to colonise experimental area 3 and diversity was low compared with other experimental areas (see Table 6).

In view of the above statement it would be more accurate to describe the intertidal community as a more or less stable system only occasionally becoming unstable when a factor such as limpet numbers (either by accident or design) changes suddenly.

At the beginning of the present study there were no differences between experimental and control areas at each Station. Both experimental and control areas contained large numbers of limpets and a low level of algal cover. The limpets were cleared from the

experimental areas and within twelve months there was extensive algal growth over most of them. The control areas were left untouched and changed very little over a period of three years. This implies that the control areas were stable and a balance achieved between the various components of the intertidal community. The experimental areas on the other hand were in an unstable condition since one of the major utilizers of the primary space, i.e., limpets had been removed. The newly available primary space was rapidly colonised by a succession of algae. These experimental areas would undoubtedly return to their previous condition after a few years and stability be regained.

A truly cyclic phenomenon would also tend to repeat itself in a more or less regular manner. If this were true fucoids should always replace limpets and vice versa. This is not necessarily the case since fucoid zygotes will not attach themselves all the year round because many of them are produced only during a limited fruiting season. Limpet spat and fucoid zygotes may both be adversely affected by severe climatic conditions. It is therefore possible that removing limpets from the primary space will simply leave bare rock since there is nothing immediately available to replace them.

Dayton (1971) stated that the components making up the intertidal community are controlled by competition between dominant species, physical disturbance and

biological disturbance. In the present study there appeared to be at least two co-dominants on the rock surface, limpets and algae both competing for primary space. A third co-dominant, barnacles, may also have influenced colonisation on certain areas.

In the control areas the two animal dominants seemed to have an advantage over the algae presumably due to the grazing activities of the limpets which created some primary space for barnacle establishment. In the experimental areas however the removal of one of the dominants (limpets) allowed one of the other dominants (algae) to increase its range. Increasing algal cover may have inhibited barnacle settlement so that their numbers declined thus increasing algal dominance even further. It is therefore likely that increasing algal cover inhibits barnacle settlement although there was no evidence to support this view from the present study.

Physical disturbance usually implies factors such as heavy wave action or adverse climatic conditions e.g., extreme heat or cold. Conditions such as these can affect both adult and larval/sporeling individuals on the shore. In the present study both experimental and control areas were subjected to the same degree of physical disturbance since they were located very near each other. Wave action damaged plants in both control and experimental areas but did not prevent re-colonisation in the experimental areas. Thus limpet grazing had a greater

effect on re-colonisation than wave action.

This statement confirms Southwards' (1964) and Thompsons' (1979) observations that limpet grazing on exposed shores prevents re-colonisation. Limpet removal therefore allows re-colonisation to take place.

Biological disturbance is shown to be a very important factor is the present study: the removal of limpets from the experimental areas changed the composition of the intertidal community in these areas. Algae covered only about 34% (average) of the rock surface before the limpets were removed but within twelve months, they covered on average 70% of most experimental areas. The control areas changed very little since a balance continued to be maintained between the co-dominants.

Connell (1972) showed that an intertidal community was made up mainly of slow-growing species. These were slow to colonise a new habitat and if removed were replaced by faster growing species. These were often ephemeral or "opportunist" species and were always present in the community to some extent. This is true of the present study. The removal of limpets from the experimental areas resulted in the rapid growth of ephemeral greens such as Enteromorpha spp. (see figures 10 and 23). These algae were already present as part of the algal community before experimentation began, and were also present in some of the control areas. They only increased

their distribution however in the experimental areas: continued grazing in the control areas prevented any increase in algal cover. The ephemeral species of Station 3 (which was subjected to severe wave action) were able to exploit the newly available primary space once the limpets had been removed. The percentage cover of E. intestinalis increased from 0% to 40% within twelve months.

Connell describes certain dominant algal species as forming a "canopy" which protects smaller, more delicate "understorey" algae which survive underneath the larger canopy plants. This description only really applies to a sheltered shore where the primary space is almost completely filled with algae. In the present study due to the exposed nature of the shore the algal cover was very sparse and there was little "canopy" available to shelter the more delicate understorey plants. In the experimental area however limpet removal produced an extensive fucoid "canopy" which allowed several red understorey species e.g., Laurencia pinnatifida and Gigartina stellata to extend their range (see figures 11, 36 and 37). This was not observed in the control areas where algal cover remained sparse.

One of the aims of the present study was to determine whether or not re-colonisation occurred on an exposed shore in a similar way to that on a sheltered shore. The results of the present study indicate the following:-

1. Limpet removal allowed algal re-colonisation on all five experimental areas regardless of physical stresses such as heavy wave action.

2. The rate of algal colonisation seemed to be affected by wave-action and run-off since re-colonisation and algal growth was noticeably slower on Station 3.

   The position of the experimental area may also have affected the rate of re-colonisation, since re-colonisation occurred normally on another exposed site (Station 5) which was situated lower down the shore.

3. There was some evidence that green algae sometimes preceded brown algae in a succession. In some experimental areas however the green algae increased their percentage cover at the same time as the browns. They did not therefore in these areas "prepare" the rock surface for colonisation by the browns.

4. The increasing fucoid canopy allowed several "under-storey" species to increase their range. On Station 1 Lithothamnion spp. increased its percentage cover from 11% in August 1974 to 20% in December 1976. Red algae such as C. tetragonum, Ceramium spp. and Gigartina stellata had colonised the surface of Station 2 during 1975: they were not present in 1974. Only G. stellata however survived to the following year. A similar situation occurred on Station 4 where several red algae

established themselves between 1974 and 1975: some of them e.g., Ceramium spp. persisted to the completion of the course of study. Several red algae extended their range on Station 5. between 1974 and 1975. G. stellata for example increased its percentage cover from 2% in 1974 to 7% in 1977, L. pinnatifida from 2% to 5% and P. palmata from 1% to 6%.

5.2 The evidence for and against cyclic changes on the experimental areas of the present study.

Southward's theory concerning the cyclic relationship between limpets and fucoids was confirmed by several other workers e.g., Thompson (1979) and Lewis (1976). It is however in some ways rather misleading since it implies a regular alternation of fucoids and limpets. There is little evidence in this or previous studies that such a cycle exists.

The most important factor in the life of an intertidal organism is living space. The organism which exploits this resource most efficiently will tend to dominate the local intertidal community. This does not mean that the domination will be necessarily long lasting or permanent.

If conditions (biotic and abiotic) remain constant, the constituents of an intertidal community will change only slightly. Harsh, physical conditions such

as those found on an exposed shore re-inforce the stability of the community since only well-adapted organisms can survive. It is only when conditions change suddenly e.g., by removing limpets that the stability is broken, fast growing species are able to exploit primary space which suddenly becomes available and the so-called cycle begins again.

It was proposed during the present study to try and determine whether or not cyclic changes occur as a matter of course in the limpet/fucoid relationship. If occurring, cyclic changes of this type might confuse the results of a clearance experiment. Algal growth was observed and compared in experimental and control areas to try and find evidence of these changes. Changes were observed in the experimental areas but were in a sense due to deliberate interference in the intertidal community. If the limpets were allowed to return to the experimental areas the intertidal community would almost certainly return to its former state i.e., the so-called "cycle" would have been completed. The experimental areas of the present study were re-examined in November 1983; almost all the alga had been removed either by wave action or limpet feeding or a combination of both.

Examination of the control areas between 1975 and 1977,

did not reveal any major changes in algal cover.

Stability was maintained by grazing and other environmental pressures such as exposure. There was no evidence of cyclic change in the control areas. The increasing fucoid levels observed in the control areas was due to fucoids growing in from adjacent experimental areas (see figures 33 and 40 for control areas). It is therefore possible to conclude that provided the co-dominants of the intertidal community are left more or less undisturbed there is nothing to prevent this stability enduring for decades.

5.3 The effect of limpet grazing on algal zonation.

The use of quantitative methods as a means of estimating the extent of algal re-colonisation made it possible to construct accurate diagrams to describe the changes that occurred on the Stations from year to year. It was possible using this method to locate new species colonising the experimental or control areas. It was also possible to observe any changes occurring in the range of a particular alga during the course of the study. The significance of changes in algal distribution and the presence of new species as a result of limpet clearance and algal re-colonisation will be discussed later in this section.

It was also proposed during the present study to determine the effect of re-colonisation on algal zonation. It has

been suggested for some time by workers such as Lodge (1952) and Southward (1978) that re-colonising algae do not form regular zones or that they form zones at different levels on the shore that they did prior to limpet clearance and re-colonisation.

Many workers agree with Connell (1972) that the upper limit of an algal zone is determined by largely physical factors e.g., desiccation and the lower limit by mainly biological forces such as grazing or competition. The observations of these workers will be compared with the results of the present study. The probability of a subtle interation between biological and physical factors and its effect on zonation will also be discussed.

Lodge noted that a member of the Rhodophyceae Dumontia incrassata increased its vertical range on the experimental strip. This rather delicate alga is normally found in damp habitats e.g., rock pools near low water mark. It was believed that increased fucoid growth allowed the Dumontia to increase its vertical range due to extra protection from the larger brown algae. This would not have been possible before limpet clearance. This was confirmed from observations made on Station 1. This experimental area was a fairly long strip of rock extending from high water mark to mid-tide level. Two members of the Rhodophyceae, Gigartina stellata and Polysiphonia spp. were absent from the experimental area in 1974. One year later G. stellata

had colonised the rock surface almost into the Pelvetia zone and Polysiphonia spp. had increased its range horizontally (see figure 10).

The colonisation of the experimental areas and subsequent growth of dense masses of fucoids probably changed the habitat on the rock surface. Prior to limpet clearance it was rather an inhospitable environment with little shelter for flora or fauna from wave action or desiccation. Increased fucoid growth might be disadvantageous for organisms such as settling limpet spat but it would provide an ideal environment for adult limpets moving in from the surrounding grazed areas. Damp conditions under the protective fucoid fronds would allow them to continue feeding even at low tide.

Other organisms such as crabs (Carcinas maenas) and sea anemones (Tealia sp.) were also observed from time to time. The latter can be regarded as an indicator animal for a damper environment since it is normally confined to permanent rock pools on the lower shore. Yet it was found attached to rock on the experimental area of Station 1. This animal was not found on any control area and its presence strongly suggests changes in the environment probably brought about by increased algal growth. Lewis (1954) observed that limpets will migrate downwards towards low water mark during the summer months to avoid desiccation. Studies of limpet movement in re-colonised

areas showing increased algal growth might have revealed modifications in this behavioural pattern. This in turn would probably affect algal colonisation due to changes in feeding patterns. It is therefore possible to conclude from these results that algal (and possibly animal zonation) can be affected indirectly by removing a grazing animal from a habitat. The resulting increase in algal growth may change a habitat to such an extent that it influences the distribution of other organisms living within it.

Pyefinch (1943) cleared one rock of A. nodosum. After re-colonisation he observed that the dominant alga on the rock was F. vesiculosus not A. nodosum as expected. This phenomenon was not observed on any of the present experimental areas. The main colonists of the experimental areas being F. spiralis and F. vesiculosus, which were also the dominant species of surrounding and control areas.

Lodge also described the apparent breakdown of zonation on her experimental areas. Three fucoids namely, F. vesiculosus, F. serratus and Himanthalia elongata, instead of forming distinct zones were observed growing mixed together in the same area

H. elongata was observed on experimental areas 2 and 5 of the present study. This alga was only noted on one occasion, February 1975 on Station 2 when it occupied 1% of the total area. On Station 5, H. elongata

increased its range between 1974 and 1976 until it reached a maximum of 15% cover. Station 2 was however placed higher up the shore than Station 5 and therefore provided a less suitable environment for the establishment of a lower shore alga such as H. elongata. It never developed into a distinct zone but grew between the fronds of other algae. This could be interpreted as confirmation of Lodge's observations. H. elongata does not withstand desiccation as well as other fucoids e.g., F. vesiculosus. The increase in its percentage cover could be due to the growth of a protective canopy which provided favourable conditions for its colonisation.

There was very little evidence for this phenomenon on any of the other experimental areas under consideration in the present study. This may be due to the fact that Lodge's experimental strip was from mid to lower shore whereas almost all the experimental areas of the present study were in the upper to mid shore (Station 5 was an exception being situated in the mid to lower shore). It is also possible that increased exposure and the steeper slopes of the experimental areas of the present study resulted in the algae forming distinct zones.

The lack of grazing after limpet clearance in Lodge's experiment may have had a greater effect on the algae due to the position of the experimental areas on the lower shore. In addition to this Lodge's experimental areas were very flat so that wide expanses of rock would have

very similar tidal regimes. This could result in a merging of algal zones as described by Lodge.

At Station 1 in the present study the experimental area had a zone of P. canaliculata, followed by a sone of F. spiralis and a very long zone of F. vesiculosus. There was also a small quantity of F. serratus on the lowermost edge of the area. The control area was too small to show zonation being entirely within the F. vesiculosus zone. However, observation of zonation in 1974 before clearance showed that no change in zonation occurred.

There was no evidence to suggest any changes in zonation at Station 2 either. This area was more or less entirely within the F. vesiculosus zone. There was no mixing of F. spiralis with F. vesiculosus for example although there were a few F. serratus plants in a gully at one end of the experimental area. These were probably able to survive in this particular corner due to run-off from nearby rock pools. The control area showed no zonation but was entirely within the F. vesiculosus zone.

Station 3 showed clear zones of three algae, P. canaliculata at the top followed by F. spiralis and a fairly long zone of F. vesiculosus. The control area produced very little algal growth and no zones of any kind. The results at this Station indicate that zonation can be established on bare rock in the absence of a grazing animal. There was no

evidence for the mixing of zones as reported by Lodge.

The experimental area of Station 4 was below the Pelvetia zone and subsequently there were no Pelvetia plants present in this area. F. spiralis and F. vesiculosus grew strongly into large "mats" but did not develop clear cut zones. The two species grew side by side as large virtually homogeneous "mats" along the length of the experimental area. This phenomenon was not observed in the adjacent control area. There was however very little algal growth in the control area and it was not possible to make a very detailed comparison between experimental and control areas. The absence of clear zones in the experimental area may have occurred because the species of algae dominating the experimental area vary in their tolerance to exposure.

It is possible that the absence of selective grazing by limpets prevented the dominance of F. vesiculosus over F. spiralis so that a zone of F. vesiculosus did not develop and both species were co-dominant on that particular area. This phenomenon was not observed on any other experimental area. The fissured rock surface (which was also tilted) may have produced a combination of dry and moist areas which resulted in a mixed zone of F. vesiculosus and F. spiralis. It is also true that a mixing of two species is possible at the boundary between two zones. The vertical extent of the experimental area of Station 4 was not however very large therefore the

apparent mixing of two algal zones may not be significant.

Zonation of brown algae was well developed at Station 5 F. vesiculosus formed a wide zone and was partly replaced by H. elongata only at the lower end of the experimental area, (see figures 36 and 37). Members of the Rhodophyceae were common in this experimental area they also showed a type of zonation although many species were found throughout the area. The control area appeared to be entirely within the F. vesiculosus zone. Observation of zonation in 1974 (before clearance) showed that no change in zonation occurred. The control area could not be used for comparison to show changes in zonation.

It is, therefore, possible to conclude from these results that limpet removal allows algal re-colonisation on exposed shores and generally normal zonation to occur. It is likely that the dominant factor controlling zonation on exposed shores is tolerance to exposure and desiccation. Limpet grazing appears to be the most important factor controlling colonisation but it is probably not as important in controlling zonation. Limpets are believed to graze on virtually any edible material found on the rock surface and they are not thought to be particularly selective in their feeding habits.

The present results indicate that only truly selective feeders affect zonation on exposed shores to any appreciable extent. Sea urchins off the coast of Canada graze

selectively on Laminaria spp. thus allowing another alga Agarum cribosum to increase its range. (Mann 1972). Limpets could only produce a similar effect if they were selective feeders.

The apparent partial breakdown of zonation as reported by Lodge in 1948 can also be explained by considering factors other than absence of limpet grazing, e.g., different algal growth rates. The more sheltered conditions and very gentle slope at Port Erin might have allowed a more varied, quicker growing flora to become established than on the rather exposed experimental areas of the present study. The absence of factors such as heavy wave action might have allowed rapid growth which would probably not result in zonation at first.

Dayton (1971) observed that any disturbance to the intertidal community resulted in changes in the distribution of certain understorey algae. This was observed in the present study to a limited extent, when for example on Station 1 D. incrassata and G. stellata were found outside their normal range.

Dayton explained this by suggesting that if a dominant species (presumably an alga) was removed, other dominants would move in to exploit new growing space. This would almost certainly result in some re-adjustment of zone boundaries. Dayton came to these conclusions by studying

sheltered shores with dense algal cover. At the beginning of the present study algal cover was sparse on all sites and there was no noticable competition between algal for growing space.

Each algal species occupies a specific micro-habitat within the intertidal habitat. Any increase in the size of the micro-habitat will almost certainly result in an increase in the distribution of the alga. Limpet clearance allows fucoids to form dense mats which maintain a moist layer on the rock surface. This allows the more delicate algae to survive higher up the shore than they would normally.

The physical conditions of the micro-habitat, which allow the red algae to survive, would not have occurred without the biological disturbance created by limpet removal and algal re-colonisation.

The results of the present study also confirm Connell's (1972) observations, that the upper limits of an algal zone can be raised by increasing moisture levels. Understorey species such as G. stellata and L. pinnatifida extended their range after canopy species became well established at Station 5.

There is some difficulty finding reasons for the establishment of the lower limit of an algal zone. On sheltered shores, where there is dense algal cover, mainly

due to lack of limpet grazing, it is likely that competition between dominants decides the demarcation line between algal zones. On exposed shores, where algal cover is sparse, it is difficult to see how the lower limit of a zone can be due to competition, since there is plenty of room for growth. Nevertheless, as the present results indicate, zonation is present on exposed shores (both before and after limpet clearance): it is likely that physical factors sush as exposure and desiccation are more important than biological factors such as competition. Once algae begin to grow as a result of limpet clearance then there may be competition for space; this may determine the lower limits of a zone.

Southward (1978) observed that re-colonisation of rock surfaces after the Torrey Canyon oil spillage resulted in the re-establishment of distinct algal zones. Certain algal zones were, however, higher up the shore than they were previously. When limpets returned to the re-colonised areas these zones were grazed back to more normal levels. These observations were not confirmed by the results of the present study, since the level of algal zones remained almost unchanged in the experimental areas. In other words the absence of limpet grazing in the experimental areas did not seem to affect normal zonation patterns.

Southward's results suggest that limpet grazing might be partly responsible for maintaining the level of certain algal zones on the shore. The thick stands of alga

formed as a result of re-colonisation, increased moisture levels on the rock surface. This enabled certain algal species to extend their range and zone boundaries. When the limpets returned, the protective "canopy" of fucoids was grazed down.

This resulted in a die back of the understorey algae down to their normal levels on the shore. This phenomenon would not normally be seen since the shore under consideration was in a state of instability due to the loss of the main herbivore. The changes observed by Southward were a temporary and to some extent an abnormal situation.

The results of the present study indicate that limpet grazing is not an important factor in establishing zonation of the dominant canopy species. They affect indirectly the distribution of some of the understorey algae which extended their range in the absence of grazing. It is therefore likely that physical factors have a greater effect than biological factors on the experimental areas of the present study since all were located on an exposed shore. Competition cannot always be ruled out however, especially in the densely colonised experimental areas.

The greatest increase in species number occurred at experimental area 2 (see Table 6). This was the least exposed site and kept moist due to run-off from nearby pools. There was less wave action and desiccation making

algal re-colonisation more likely. The increase in species number was only 10% (an increase of two new species) in the corresponding control area. The only difference between the two areas was the absence of limpet grazing from the experimental area. The increase in species number observed at each experimental area indicates that lack of grazing increases the species diversity of the intertidal flora. This is probably due to the development of a protective fucoid canopy and the resulting growth of understorey species.

Station 3 showed the lowest increase in species number. Only five species colonised the area in three years. The control area showed virtually no growth, only one species colonising in three years. This Station was very steep and subjected to severe wave action and run-off. This must have badly affected spore settlement and re-colonisation in both experimental and control areas. The absence of limpets did however allow algal growth on the experimental area but species diversity was low. Therefore, abiotic factors affect species diversity, limpets are not the only factor reducing species diversity.

As a rule, the increase in species number is greater in the experimental areas than in the control areas (see Table 6). Most of the increase is due to increased moisture levels on the rock surface provided by the fucoid canopy since many of the "new" species were

"understorey" algae. This increase would not have occurred without limpet removal.

It is possible that the absence of limpet grazing allows new species to colonise the rock surface. The "new" species colonising the experimental areas are sometimes found in the control areas where grazing already occurs, e.g., P. umbilicalis was a new species on experimental area 1 in 1975; this alga was also present in the control area (see Table 6). It is therefore likely that other factors such as an increase in moisture must be taken into consideration. Colonisation appeared to be complete on all experimental areas by 1976 since no new species were observed after this date.

In conclusion it is possible to state that re-colonisation and algal zonation is basically the same on both exposed and sheltered shores. The rate of colonisation is slower on exposed shores due to wave action and run-off preventing spore settlement. Algal zonation does not appear to be affected by lack of grazing and re-colonisation. Comparisons made between the experimental areas and adjacent rock surfaces (not the controls) indicated that algal zones were established normally.

Investigations of shore phenomena such as re-colonisation and zonation reveal that the intertidal habitat is in a constant state of flux. Constantly changing physical and biological factors are responsible for this. It is becoming increasingly difficult to differentiate between

the effects of physical factors on the one hand and biological factors on the other since both interact in their effect on living organisms.

5.4 Further Work

Future work could include more detailed investigations into the stages involved in the colonisation of a rock surface once the fucoid canopy is established; this usually occurs about twelve months after the initial limpet clearance. The succession of the smaller understorey algae could then be established. Much smaller experimental areas could be chosen so that the total area under investigation could be examined more quickly and on a more regular basis.

Algal colonisation was also probably affected by rather sporadic limpet clearance carried out during the period of study. Smaller experimental areas would make regular clearance more thorough and much more effective.

It would also have been useful to estimate barnacle numbers on the various experimental areas. This would have given some indication of the effect of increasing fucoid cover on barnacle numbers. There is still some controversy as to whether weathering is necessary before colonisation can take place. A more detailed investigation of the brown "slime" which develops after limpet clearance and before algal colonisation may reveal a

a "micro-succession" which may be a precursor to colonisation, i.e., a type of weathering.

It might also have been useful to have carried out clearance experiments at various times of the year apart from the summer months. This might have resulted in a different succession pattern.

There is still much that remains to be investigated about the conditions necessary for spore settlement. This would involve laboratory experiments as well as shore investigations.

The control areas were too small to compare with the experimental areas with respect to algal zonation. Future work should include longer control areas parallel with the experimental areas and separated from the latter by a "buffer" zone to prevent algal growth encroaching.

The experimental areas could also be investigated in detail when colonisation is complete and the limpets allowed to return. It would then be possible to establish which algal species are particularly vulnerable to limpet grazing since these would be grazed down first.

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